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Article

Dispersal traits as benthic invertebrate assemblage drivers in a neotropical large river

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With 2 figures and 2 tables

Abstract: Metacommunity theory is a mechanistic framework that explains the interdependence of local factors and regional processes as community drivers. Recent evidence suggests that dispersal mode is a key trait that potentially affects metacommunity dynamics. We analyzed the distribution patterns of benthic macroinvertebrates with different dispersal modes in the Middle Paraná, a neotropical large river. We assessed the relative importance of local environmental conditions and regional spatial structure as assemblage drivers. Aquatic and aerial dispersers presented Clementsian and Gleasonian structures, respectively. For both groups, local environmental conditions influenced community assembly, and spatial structure (overland distances) also affected the distribution of aerial dispersers. Our study highlights that the role of spatial structure as a driver of benthic metacommunities depends on species' dispersal modes. Aerial dispersers responded to regional spatial variables and it is likely that these organisms are also influenced by mass effects. Our results are consistent with current ideas of metacommunity dynamics in large rivers, where dispersal is not considered to limit the distribution of benthic organisms.

Keywords: Chironomidae; floodplain; macroinvertebrates; mass effects; metacommunity; Oligochaeta

Introduction

Metacommunity theory provides a mechanistic framework that explains the interdependence of local factors (e.g. environmental conditions and biological interactions) and regional processes (e.g. dispersal) as community drivers. Recent metacommunity research has followed approaches including analysis of the 'elements of metacommunity structure' (EMS), which focuses on three characteristics of species distribution, namely coherence, turnover and boundary clumping (Leibold & Mikkelson 2002). Based on these parameters, patterns of species distributions within metacommunities can be characterized as random, checkerboard, nested, Clementsian, Gleasonian or evenly spaced. In random metacommunities, species distribution does not differ from null expectation and niche-based processes have little influence. Checkerboard metacommunities (Diamond 1975) comprise pairs of mutually exclusive species, suggesting a strong effect of competitive exclusion. Competition may also be an important driver in evenly spaced metacommunities, in which species are uniformly distributed along an environmental gradient (Henriques-Silva et al. 2013). In nested metacommunities, species-poor communities are subsets of richer ones, which may reflect gradients of environmental harshness (Henriques-Silva et al. 2013). In Clementsian metacommunities, species form groups that replace each other along an environmental gradient. These structures may be caused by sharp environmental gradients or biological interactions such as mutualism and predation (Wojciechowski et al. 2017). Conversely, the species in Gleasonian metacommunities have idiosyncratic responses to environmental gradients, suggesting that these gradients may be less steep.

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Since the seminal paper of Leibold & Mikkelson (2002), the EMS approach has been widely applied in different ecosystem types (Presley et al. 2009; Heino et al. 2012; Henriques-Silva et al. 2013; Fernandes et al. 2014; Petsch et al. 2017). However, EMS analysis alone may be insufficient to disentangle the ecological processes that shape metacommunities (Schmera et al. 2018). An approach that complements EMS involves assessing the relative importance of spatial and environmental factors as community drivers (Smith & Lundholm 2010; Winegardner et al. 2012). This approach assumes that the effects of local environmental conditions on biological communities indicate the importance of niche-based processes as a structuring factor (Cotennie 2005; Heino et al. 2010). Equally, the effects of spatial structure indicate the importance of regional community drivers such as species' dispersal abilities, landscape configuration and connectivity (Cañedo-Argüelles et al. 2015; Heino et al. 2015a; Phillipsen & Lytle 2013; Tonkin et al. 2018). There is growing evidence that niche-based processes may be more important than spatial structure in determining metacommunity composition, although there is considerable variability among systems (Heino et al. 2012; Algarte et al. 2014; Sarremejane et al. 2017).

Metacommunity characterization is especially challenging in large floodplain rivers. These rivers are highly heterogeneous environments which may place a strong environmental control on biological assemblages. Conversely, water bodies in this type of system are highly connected, which can potentially blur the effects of environmental controls. As a result, metacommunity studies performed in large rivers have reported contrasting results (Fernandes et al. 2014; Devercelli et al. 2016; Dias et al. 2016; Petsch et al. 2017).

Recent research has demonstrated that the analysis of biological traits can improve understanding of the observed variability in metacommunity composition by providing a more mechanistic understanding of habitat filtering and dispersal limitation (McGill et al. 2006). Dispersal mode is an especially important trait, because it may influence species' responses to environmental gradients and thus metacommunity structure (Grönroos et al. 2013; Heino et al. 2015a). Accordingly, several analyses performed in different ecosystem types have reported that assemblages dominated by species with different dispersal modes may present different metacommunity structures (De Bie et al. 2012; Padial et al. 2014; Saito et al. 2015). However, most studies have been conducted in small streams and/or in temperate regions, and information about large neotropical rivers remains scarce (Petsch et al. 2017). In such ecosystems, benthic macroinvertebrates have contrasting dispersal strategies, for example drift (i.e. passive aquatic dispersal) is the main mode used by species of Oligochaeta, Mollusca and Crustacea, whereas many insects exhibit active aerial dispersal. In lakes of the Upper Paraná, a large neotropical river, Petsch et al. (2017) found that macroinvertebrate assemblages of species with passive and active dispersal strategies differed in their metacommunity structure. The random structure of passive dispersers implied that environmental heterogeneity was not an important driver of community structure (Petsch et al. 2017).

In the present study, we focused on benthic macroinvertebrates that inhabit the beds of rivers and floodplain lakes of the Middle Paraná River. Our first aim was to determine if assemblages of species dominated by aerial and aquatic dispersers differ in their metacommunity structure. Our second aim was to examine the relative importance of local environmental conditions and regional spatial structure as drivers of metacommunity structure for aerial and aquatic dispersers.

Methods

Study area and field methods

The Paraná River is a large South American river that flows for 4400 km (Paira & Drago 2007), of which the 1000 km furthest downstream are unregulated. The study area is located 10 km east of Santa Fe city (Argentina), 500 km downstream of the nearest dam (Yacyretá) where the river has characteristics typical of a large free-flowing river (Iriondo et al. 2007). We selected 30 perennial water bodies including four main channels with discharge > 4000 m^3 s^{-1}) eight secondary channels with discharge between 100 1700 m^3 s^{-1}, 12 isolated and six connected floodplain lakes (Fig. 1). Samples were collected in November 2013, during a normal seasonal low-flow phase.

At each sampling site, we measured depth, temperature, dissolved oxygen (DO, Hanna meter HI-9146), pH (HI-991003), conductivity (HI-9033), and transparency (Secchi disk). We also collected a drag sample (225 cm^2) at each site, to measure the proportion of sand in sediments and the sediment organic matter content % by loss on ignition for 3 h at 550 °C. The aquatic vegetation at each site was surveyed by boat, with the total macrophyte cover estimated using a percentage scale. The macrophytes were surveyed using quadrats (1 m × 1 m) that were placed along transects perpendicular to the shoreline. Within each transect, the distance between successive quadrats was constant, and the number of quadrats per transect varied from one to 16 according to the length of the macrophyte stand (Schneider et al. 2015; Devercelli et al. 2016). Because the beds of rivers and lakes in the Paraná system are mainly composed of mud and silt, we used Ekman grabs (225 cm^2) to collect three macroinvertebrate samples from the centre of each lake or channel. This method has been demonstrated as effective in soft sediments (Lewis et al. 1982) and is appropriate to sample

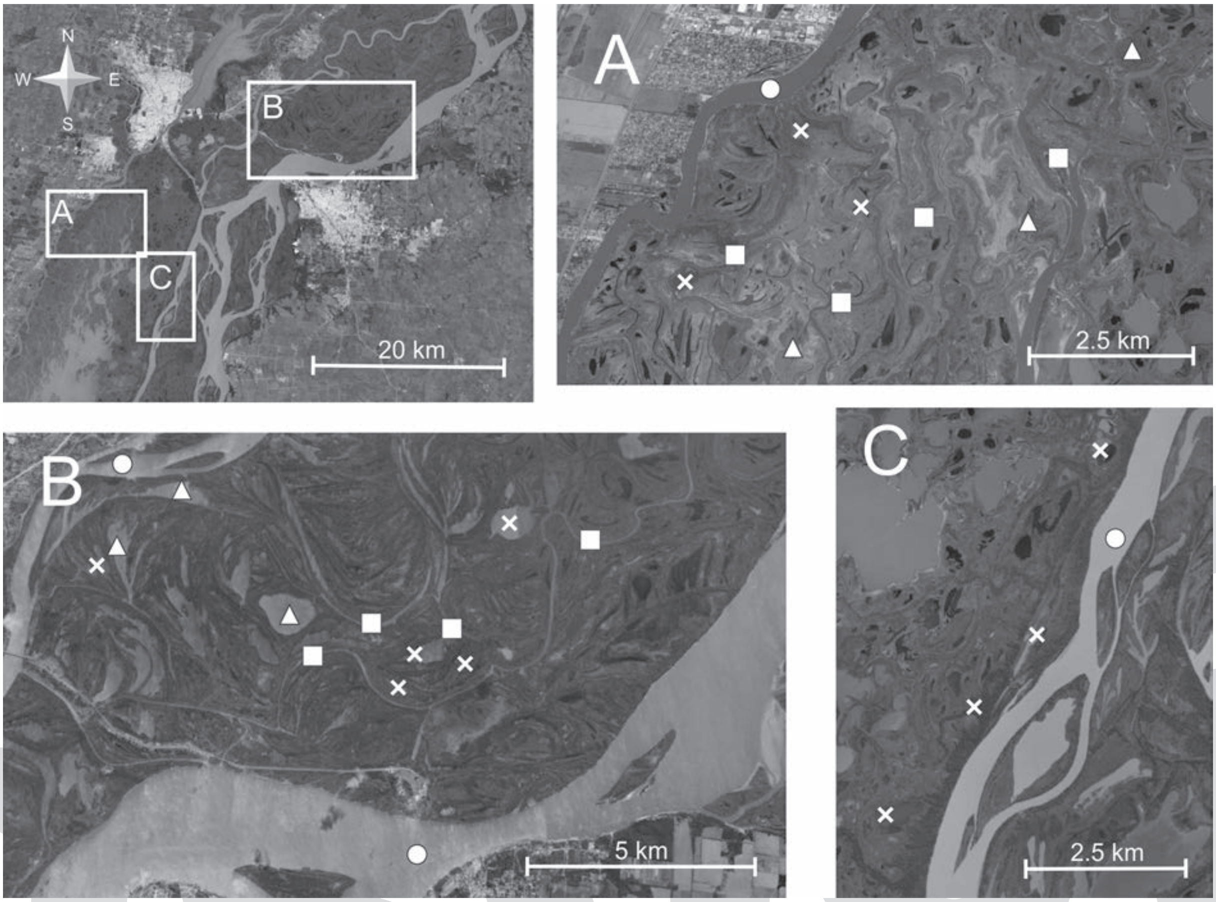

Fig. 1. Study area in the Middle Paraná River. Filled circles = main channels, squares = secondary channels, triangles = permanently connected lakes, crosses = isolated lakes.

taxa that dominate assemblages in the Middle Paraná River, i.e. Oligochaeta, Turbellaria and Chironomidae (Diptera; Iriondo et al. 2007). Samples were filtered through a 200-µm sieve and fixed with 10 % formaldehyde in the field.

In the laboratory, macroinvertebrates were handpicked under a stereoscopic microscope (4×) and preserved in 70 % ethanol. Taxa were identified to the lowest taxonomic level possible (genus or species) using Brinkhurst & Marchese (1991), Domínguez & Fernández (2009) and Trivinho-Strixino (2011). Using information from Lopretto & Tell (1995) and Domínguez & Fernández (2009), each taxon was classified according to its dispersal mode as an aquatic or aerial disperser, with both active and passive dispersers included in each category.

Elements of metacommunity structure

We compared the distribution of benthic taxa using the EMS framework (Leibold & Mikkelson 2002). The first step in EMS is the ordination of a taxa distribution matrix (sites by taxa), here using correspondence analysis (CA) that maximized the positioning of sites along axes based on the degree to which their communities shared taxa and the positioning of taxa sharing a similar range (Leibold & Mikkelson 2002). Species and sites were ranked according to their position on CA axis 1. The second step is the analysis of coherence, which is measured as the number of embedded absences in all taxon ranges and community compositions. If this parameter is lower than null simulations, metacommunity patterns are characterized by a checkerboard structure, whereas non-significant coherence indicates a random structure. When the observed number of embedded absences in all taxon ranges and community compositions was higher than expected by chance, taxonomic turnover was evaluated. If turnover is lower than the mean of null simulations then the metacommunity is considered as nested. Conversely, where turnover was higher than the mean of null simulations, boundary clumping was assessed using the Morisita index (Morisita 1971), which has a null expectation of 1. Where the observed index did not differ from 1, randomly distributed community boundaries indicated a Gleasonian structure; low index values indicated an evenly spaced structure because community boundaries are over dispersed; and index values significantly higher than 1 indicated Clementsian metacommunities. Analyses were performed in R version 3.4.3 (R Core Team 2017) using the *Metacommunity* function in the *metacom* package (Dallas 2014).

Variance partitioning

We used variance partitioning analysis to separate the fractions of variation explained by spatial structure and local environmental conditions (Borcard et al. 1992). We used partial redundancy analysis (RDA) to assess associations between community composition and variables of one group controlling associations with variables of other groups (shared and residual components are not testable; Legendre 2008).

We also assessed the relative importance of environmental and spatial variables as community structuring factors using partial RDA. We used two models for both aerial and aquatic dispersers. In both models, biological data were Hellinger-transformed incidence matrices (sites by taxa), and environmental data comprised the standardized variables (mean = 0 and unit variance) measured in the field (depth, temperature, DO, pH, conductivity, transparency, total macrophyte cover, sand, organic matter). In the first model, the spatial component was the overland distances among sampling sites, described using a Euclidean distance matrix. This distance matrix was then submitted to a Principal Coordinate Analysis of Neighbour Matrices (PCNM) whose axes (eigenvectors) represent a spectral decomposition of the spatial relationships among sampling sites. These axes correspond to all the spatial scales that can be detected in a given dataset (Borcard & Legendre 2002; Borcard et al. 2004). In the second model, the spatial component was the watercourse distance (i.e. network distance, sensu Brown & Swan 2010) among water bodies, accounting for flow directionality using asymmetric eigenvector maps (AEM). The AEM framework creates eigenvectors that correspond to an asymmetric, directional process, such as watercourse dispersal. These axes also represent the spatial scales that can be detected in the dataset and can be used as explanatory variables in multivariate analysis (Blanchet et al. 2007). For both spatial (overland and watercourse) distances and environmental matrices, we performed a forward selection procedure to select the most important variables, as suggested by Blanchet et al. (2008).

Results

Environmental variables showed substantial variability among sampling sites. While depth and macrophyte cover showed the highest coefficients of variation, temperature and pH were least variable (Table 1). Depth was highly variable, reflecting sampling in both deep rivers (11 m) and shallow lakes (0.5 m). Similarly, some lakes were almost completely covered by macrophytes, whereas macrophytes were absent in some rivers.

We sampled 7697 individuals belonging to 58 taxa, of which 22 (1567 individuals) were aerial dispersers and 36 (6130 individuals) were aquatic dispersers. The most abundant aerial dispersers were *Polypedilum* sp. (16 %), *Chironomus* sp. (14 %), and *Caladomyia ortoni* (11 %; all Diptera: Chironomidae). The most abundant aquatic dispersers were *Narapa bonettoi* (23 %; Oligochaeta: Narapidae), *Aulodrilus pigueti* (14 %) and *Limnodrilus hoffmeisteri* (13 %; both Oligochaeta: Tubificinae). Oligochaeta (Naididae and Narapidae) were the most abundant group (74 % of individuals) followed by Chironomidae (20 %). Other common families were Polymitarcyidae (Ephemeroptera), Hyallelidae (Amphipoda), Corbiculidae (Bivalvia), Retronectidae (Catenulida), Cochliopidae (Caenogastropoda) and Hydridae (Cnidaria). Some species, such *as N. bonettoi*, *Myoretronectes paranensis* (Retronectidae), *Itaspiella* sp. (Turbellaria: Otoplanidae) and *Tobrilus* sp. (Nematoda: Tripylidae), were only recorded in rivers. Other species, such as *Dero sawayai* (Naididae), *Campsurus violaceus* (Polymitarcyidae) and *Polypedilum* sp., were only present in floodplain water bodies.

Table 1. Mean ± standard deviation (SD) and coefficient of variation (CV) for environmental variables measured at each sampling site.

	Mean	SD	CV
pH	7.44	0.56	0.08
Conductivity (μs cm^{-1})	148.73	85.91	0.58
DO (%)	61.16	30.60	0.50
Transparency (cm)	0.37	0.22	0.59
Depth (m)	2.60	2.76	1.06
Macrophyte cover (%)	25.56	28.12	1.10
Sand (%)	80.06	13.85	0.17
Organic matter (%)	2.19	1.51	0.69
Temperature (°C)	26.96	1.62	0.06

Elements of metacommunity structure

Both aerial and aquatic dispersers showed higher coherence than expected by chance along the environmental gradient, indicating coherent ranges (Table 2). The turnover of both groups was higher than the mean simulated. The Morisita index of aquatic dispersers

Table 2. Results of the elements of metacommunity structure analysis of aquatic and aerial dispersers. Coherence is measured as embedded absences. Boundary clumping is measured with the Morisita index.

		Simulated	Observed	*p*	Structure
Aquatic dispersers	Coherence	668	461	< 0.001	Clementsian
	Turnover	1229	1633	0.07	
	Boundary clumping		1.4	0.002	
Aerial dispersers	Coherence	335	198	< 0.001	Gleasonian
	Turnover	6003	6892	0.49	
	Boundary clumping		1.26	0.07	

was >1 and metacommunity structure was thus characterized as Clementsian, whereas the index of aerial dispersers did not differ from 1 and metacommunity structure was considered to be Gleasonian (Table 2).

Variance partitioning

For aquatic dispersers, depth was the only selected environmental variable after the forward selection procedure (partial RDA, $p = 0.001$). Overland distance performed poorly, as no PCNM axis was selected. Moreover, AEM eigenvector 2, which represented spatial structure at a broad scale, was selected. Partial RDA yielded significant results only for local environmental conditions. Depth was also the only selected variable for aerial dispersers (partial RDA, $p < 0.05$). Watercourse distance was a poor predictor for this group, as no AEM vector was selected. However, PCNM axes 2 and 7, which accounted for overland distances among sites, were selected. The partial RDA showed that both local environmental conditions and overland distances among sites were significant drivers of assemblages of aerial dispersers (partial RDA, $p < 0.05$). For both groups, a large proportion (89 %) of variance was unexplained (Fig. 2).

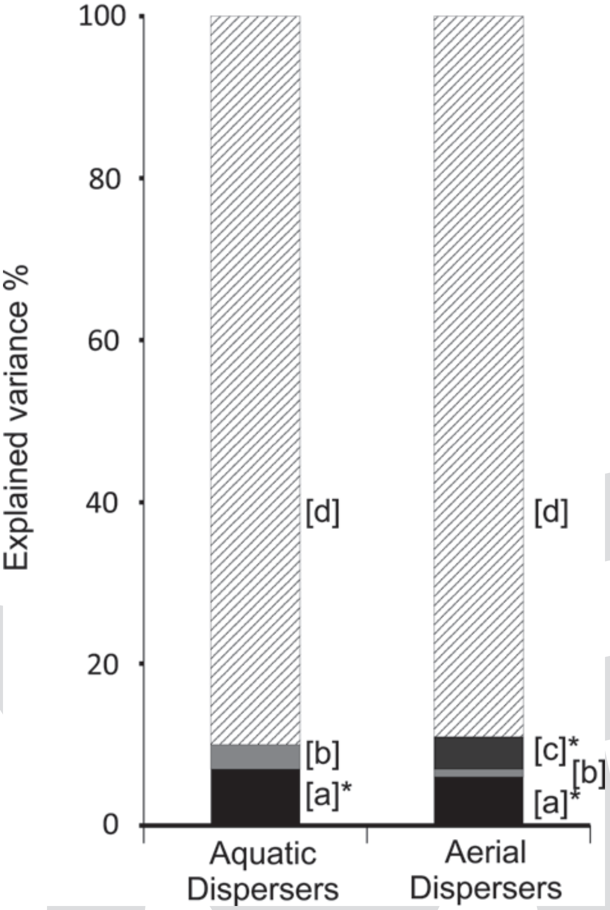

Fig. 2. Variance partitioning for aquatic and aerial dispersers. **[a]** = environmental component, **[b]** = component shared between environmental and spatial components, **[c]** = spatial component, **[d]** = residuals; *, significant values ($p < 0.05$).

Discussion

In our study of a large neotropical river system, freshwater invertebrates with both aerial and aquatic dispersal strategies presented coherent distribution ranges and replaced each other along environmental gradients. However, aquatic dispersers comprised discrete assemblages (Clementsian structure) whereas aerial dispersers showed idiosyncratic responses to environmental gradients (Gleasonian structure). Heino et al. (2015b) hypothesized that species in more disturbed systems should show more individualistic responses to environmental gradients than species in more stable lentic systems. Gleasonian metacommunity types should thus prevail in lotic freshwaters (Heino & Soininen 2005), whereas Clementsian metacommunities should be more common in lentic systems.

Clementsian patterns may be among the most common metacommunity structures in freshwater ecosystems (Henriques-Silva et al. 2013). Previous studies have reported these structures for benthic macroinvertebrates (Heino et al. 2015b; Petsch et al. 2017) and fish (Fernandes et al. 2014). Gleasonian structures are less frequent, but have been reported for snails (Hoverman et al. 2011) and fish (Henriques-Silva et al. 2013), and beyond the freshwater realm for bats (López-González et al. 2012; Cisneros et al. 2015) and marsupials (de la Sancha et al. 2014). Some authors have hypothesized that Clementsian metacommunity structures should prevail in stable environments (Heino et al. 2015b) such as lentic water bodies. This aligns with our results for aquatic dispersers, since 18 of our 30 sites were lakes. Another explanation for Clementsian structures is that species can only coexist in certain combinations, with others “forbidden” by interspecific interactions (Gilpin & Diamond 1982). However further research involving phylogenetic approaches may be necessary to disentangle the role of competition in this type of metacommunity (Mason et al. 2008; Henriques-Silva et al. 2013).

Although both aerial and aquatic dispersers showed gradient structures, our results contrast with those of Petsch et al. (2017), who reported a random structure for passive aquatic dispersers in floodplain lakes of the upper Paraná. This difference could be because we sampled both floodplain lakes and rivers (including main channels) and thus covered a wider range of environmental conditions. These habitats differ in their physical conditions and biological assemblages, for example main channels are characterized by high drag forces, low sediment organic matter content and sandy substrates. In the Paraná River, species that are adapted to these conditions and inhabit the main channels are absent from floodplain lakes, for example *Narapa bonettoi*, *Rhyacodrilus* sp. (Naididae), *Myoretronectes paranensis* and *Tobrilus* sp. (de Drago et al. 2007; Blettler et al. 2008). Equally, many taxa (e.g. *Campsurus violaceus*, *Polypedilum* sp.) are absent in main channels because they are adapted to conditions in lentic waters.

Consistent with the gradient metacommunity structures of aerial and aquatic dispersers, local environmental conditions played an important role as assemblage determinants. This aligns with a growing body of evidence suggesting local environmental conditions as among the major drivers of metacommunity structure (Cottenie et al. 2003; Fernandes et al. 2014; Petsch et al. 2017). In this study, depth was the most important environmental variable, which is unsurprising as the depth range was 0.5–11 m, including shallow floodplain lakes and deep sand-bottomed rivers. Moreover, depth is related to several important variables such as hydraulic stress (Rempel et al. 1999; Blettler et al. 2012), habitat heterogeneity (Pinel-Alloul et al. 1988) and surface area (Nõges 2009), which were not measured in this study.

The role of spatial factors differed between the two dispersal groups. For aerial dispersers, overland distance among water bodies was a significant assemblage driver. Notably, watercourse distance was a poor predictor of the benthic assemblage, suggesting that aquatic dispersal could be negligible for species with flying adults. Although flow connectivity influences the dispersal of aquatic organisms (Hughes 2007; Zawalski et al. 2019), our findings agree with Cañedo-Argüelles et al. (2015), who reported that watercourse distance did not affect macroinvertebrate community dissimilarity in a dryland river basin. In that study, the stream network was fragmented by streambed drying, and thus aquatic macroinvertebrates with flying adult life stages dispersed overland, using perennial waters as stepping stones (Cañedo-Argüelles et al. 2015). Similarly, our study was performed during a low-water period, and some sampling sites were hydrologically isolated. However, even at low water levels, the Paraná River floodplain contains numerous perennial water bodies such as ponds, wetlands and oxbow lakes, which could serve as stepping stones. Thus, even relatively weak flyers, such as adult chironomids that may disperse about 500 m from a water body (Delettre & Morvan 2000), could disperse between scattered water bodies during low-water periods.

Our aerial disperser group was mainly composed of Chironomidae larvae, which is unsurprising as this study was restricted to the beds of lakes and rivers in which this family is dominant (Ezcurra de Drago et al. 2007). Stronger aerial dispersers such as Odonata or Coleoptera are more abundant in other habitat types, such as macrophytes roots and litter patches (Ramseyer & Marchese 2009; Copatti et al. 2013). The higher dispersal rates of these taxa could imply an overriding effect of spatial structure as an assemblage driver (Heino et al. 2015a). The inclusion of litter patches and macrophytes roots in further studies could thus improve our understanding of the metacommunity dynamics of aerial dispersers in large rivers.

For aquatic dispersers, neither watercourse distances nor overland distances were significant drivers of metacommunity composition. This result agrees with previous studies in which aquatic dispersers displayed stochastic distributions, leading to weak spatial structures (Cañedo-Argüelles et al. 2015; Richardson et al. 2016). Moreover, it has been hypothesized that non-significant spatial signals characterize taxa with intermediate dispersal rates (Heino et al. 2015a). Our results suggest that, in the Middle Paraná River, dispersal is not limiting for aquatic dispersers. This aligns with current ideas about metacommunity organization in large rivers (Brown & Swan 2010) where, unlike headwaters, high connectivity among sites promotes high dispersal of organisms (Göthe et al. 2013; Göthe et al. 2017; Schmera et al. 2018).

The role of dispersal mode in structuring communities has been widely discussed (Padial et al. 2014; Saito et al. **??2014 or 2015??**; Heino et al. 2015a; Tonkin et al. 2016). Some studies have indicated that active aerial dispersers may be more influenced by local environmental conditions, because they can track environmental variability (De Bie et al. 2012; Grönroos et al. 2013). However, high dispersal rates may result in a significant spatial signal even when environmental controls are strong (Ng et al. 2009), if mass effects sustain populations at sites where their growth rate is negative (Cottenie & De Meester 2005; Heino et al. 2015a). In such cases, both environmental and spatial factors are expected to drive metacommunity structure (Ng et al. 2009; Heino et al. 2015**??a or b??**).

Our study provides evidence that environmental controls may play an important role as an assemblage driver in large neotropical rivers. This implies that environmental heterogeneity is key to maintaining the biodiversity of these ecosystems. Moreover, aerial dispersal is important even for weak flyers such as chironomids, which could thus use scattered water bodies as stepping stones to facilitate their dispersal. In this context, preserving wetlands could be crucial to maintain metacommunity dynamics in large rivers. One priority for future research is to encompass a greater range of habitat types within sampling strategies, to address the metacommunity dynamics of strong aerial dispersers in large floodplain rivers.

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Authors' contributions

MS, MM and LM conceived the idea and wrote the manuscript. MS performed the statistical analysis.

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