



# Factors affecting the metacommunity structure of periphytic ostracods (Crustacea, Ostracoda): a deconstruction approach based on biological traits

Ramiro de Campos<sup>1</sup> · Fernando Miranda Lansac-Tôha<sup>1</sup> · Eliezer de Oliveira da Conceição<sup>1</sup> · Koen Martens<sup>2,3</sup> · Janet Higuti<sup>4</sup>

Received: 10 May 2017 / Accepted: 30 January 2018 / Published online: 7 February 2018  
© Springer International Publishing AG, part of Springer Nature 2018

## Abstract

Metacommunity studies using the deconstruction approach based on biological traits have received a great deal of attention in recent years as they often better describe characteristics of the species that reflect adaptations to a specific environment. This approach has not yet been used for ostracods, which are nevertheless highly diverse crustaceans and abundant in continental aquatic environments. Here, we investigate the influence of environmental and spatial factors on the metacommunity structure of periphytic ostracods in 27 tropical floodplain lakes in the Upper Paraná River floodplain (Brazil). An analysis of variance partitioning was used to estimate the relative importance of these factors (environmental and spatial) on both the entire community as well as after its deconstruction according to the biological traits (size and locomotion mode). Ostracods, regardless of body size, are good dispersers at regional scales. In addition, as expected, swimming ostracods were better dispersers at local scales than non-swimmers, which were influenced mainly by the diversity of aquatic macrophytes. Environmental factors (species sorting mechanism) seem important in structuring the entire ostracods metacommunity, as well as for most categories of biological traits. The unexplained variability remained high showing that other variables, not measured here, must be important. The analysis based on deconstruction, when compared to the analysis based on the metacommunity as a whole, contributed to a better assessment of ostracod metacommunity structuring.

**Keywords** Microcrustacean · Dispersal · Body size · Aquatic vegetation · Partitioning · Upper Paraná River floodplain

## Introduction

For several decades, it was thought that environmental events at local scales (Ricklefs 1987), such as habitat conditions, predation and competition, determined biological

**Electronic supplementary material** The online version of this article (<https://doi.org/10.1007/s00027-018-0567-2>) contains supplementary material, which is available to authorized users.

✉ Koen Martens  
darwinula@gmail.com

Ramiro de Campos  
rami\_campos@hotmail.com

Fernando Miranda Lansac-Tôha  
fernando\_toha@hotmail.com

Eliezer de Oliveira da Conceição  
eliezer.oliveira.c@gmail.com

Janet Higuti  
janethiguti@gmail.com

de Maringá (UEM), Av. Colombo, 5790, Maringá,  
PR CEP 87020-900, Brazil

<sup>2</sup> Royal Belgian Institute of Natural Sciences (RBINS),  
Vautierstraat 29, 1000 Brussels, Belgium

<sup>3</sup> Department of Biology, University of Ghent,  
K.L. Ledeganckstraat 35, 9000 Ghent, Belgium

<sup>4</sup> Universidade Estadual de Maringá (UEM), Núcleo de  
Pesquisas em Limnologia, Ictiologia e Aquicultura (Nupélia),  
Programa de Pós-Graduação em Ecologia de Ambientes  
Aquáticos Continentais (PEA), Av. Colombo, 5790, Maringá,  
PR CEP 87020-900, Brazil

<sup>1</sup> Programa de Pós-Graduação em Ecologia de Ambientes  
Aquáticos Continentais (PEA), Universidade Estadual

community structuring (Leibold et al. 2004; Heino et al. 2015). However, currently it is known that local species diversity is also affected by ecological events at regional scales, such as dispersal potential, geological settings and climate (Göthe et al. 2016). Understanding the relevance of both environmental (local) and spatial (regional) factors determining community structuring is the aim of the metacommunity approach (Alahuhta et al. 2014). Here, we define a metacommunity as “a set of local communities that are linked by dispersal of multiple potentially interacting species” (Leibold et al. 2004).

Four main paradigms were proposed to explain metacommunity processes: species sorting, patch-dynamic, mass effect and neutral processes (Leibold et al. 2004; Gronroos et al. 2013). However, Logue et al. (2011) proposed to integrate these perspectives in future research on metacommunity ecology, since they are not mutually exclusive and different processes may act simultaneously in a metacommunity (Gravel et al. 2006). Species sorting integrates niche explanations (Hájek et al. 2011), where the abiotic features filter the set of species co-occurring in each patch, provided there is sufficient dispersal so that the species can follow the environmental variation (Leibold et al. 2004). Patch-dynamic and mass effect paradigms integrate the dispersal events: which are either limited or efficient, respectively (Hájek et al. 2011). In the neutral paradigm, finally, species are equivalent and both random and stochastic events of dispersal, extinction, speciation and colonization are responsible for structuring communities (Hubbell 2001).

Moreover, some authors have suggested that mass effects and patch-dynamics are only special cases of species sorting, according to the levels of dispersal capacity of the species concerned (Winegardner et al. 2012). Thus, in a simplistic way, metacommunity studies should be directed towards the roles of species sorting and dispersal, which are seen as the fundamental structuring processes in all metacommunities (Lindström and Langenheder 2012; Heino et al. 2015).

In general, the action and relevance of these structuring processes depends mainly on the characteristics of the biological groups under study (Pandit et al. 2009). As such, the “deconstruction approach” has been used and consists of separating the matrices of different species according to the biological traits of these organisms (Silva and Hernández 2015). Approaches based on species traits has great potential, because such specific characteristics often relate to adaptations to a specific environment (Hoeinghaus et al. 2007; Heino et al. 2015). For example, studies targeting groups of species classified according to dispersal mode (passive/weak or active/strong) have found that spatial effects are more important for the weak dispersers than for strong dispersers (Hájek et al. 2011; De Bie et al. 2012; Padiál et al. 2014). In addition to the dispersal mode, other traits such as body size (Astorga et al. 2012; De Bie et al.

2012), reproduction mode (Landeiro et al. 2014) and rarity (Pandit et al. 2009; Siqueira et al. 2011; Alahuhta et al. 2014; Petsch et al. 2015) have also been considered.

Freshwater ecosystems in general are excellent model systems to evaluate metacommunity dynamics, since they combine high environmental heterogeneity, with great variation in the connectivity and spatial extension of their environments (Heino 2011; Heino et al. 2014). Riverine floodplains are particularly good examples of systems featuring such characteristics, in addition to a generally high biodiversity (Agostinho et al. 2004). Ostracods are abundant in such ecosystems and inhabit a variety of habitats, such as benthic regions, littoral and submerged macrophyte stands, as well as the roots of floating aquatic macrophytes (Higuti et al. 2007; Liberto et al. 2012; Higuti and Martens 2016). In the latter case, such root systems provide food, shelter from predators and general substrates for reproduction (Thomaz and Cunha 2010).

Ostracods are small microcrustaceans ranging from c 0.3–c 5 mm in the Neotropical, and all species disperse exclusively in a passive way over long distances, either as torpid juveniles and adults or as drought resistant eggs (Meisch 2000; Martens et al. 2008). However, there are major differences in the locomotion mode, as some species can swim (with long natatory antennal setae), while other species lack such natatory setae and can only move by crawling over substrates (Meisch 2000) and this can make a difference at smaller scale dispersal. Recent studies on ostracod metacommunities (Escrivà et al. 2015; Zhai et al. 2015; Castillo-Escrivà et al. 2016a, b, c, 2017) have evaluated entire communities as such, but did not focus on individual biological traits.

Here, we investigate the effects of environmental and spatial factors on ostracod metacommunity structure. We first analyse the entire community and subsequently apply deconstruction according to the biological traits (body size and locomotion mode). We address two questions: (1) are ostracods of different body sizes and locomotion mode influenced by different factors? and (2) does the deconstruction analysis based on biological traits increase the explanatory power of the environmental and spatial factors on ostracod metacommunity structure?

Taking into account the dispersal mode of ostracods (passive) and based on the assumption that the increasing body size decreases the possibilities for passive long-distance dispersal of the organisms (De Bie et al. 2012), we expect that the larger the body size of ostracods, the greater the influence of the spatial factors. In addition, swimming ostracods are expected to be better dispersers at local scales than non-swimmers and will be more influenced by environmental factors. Finally, we also evaluate the ostracod species composition on different macrophyte species.

## Materials and methods

### Study site

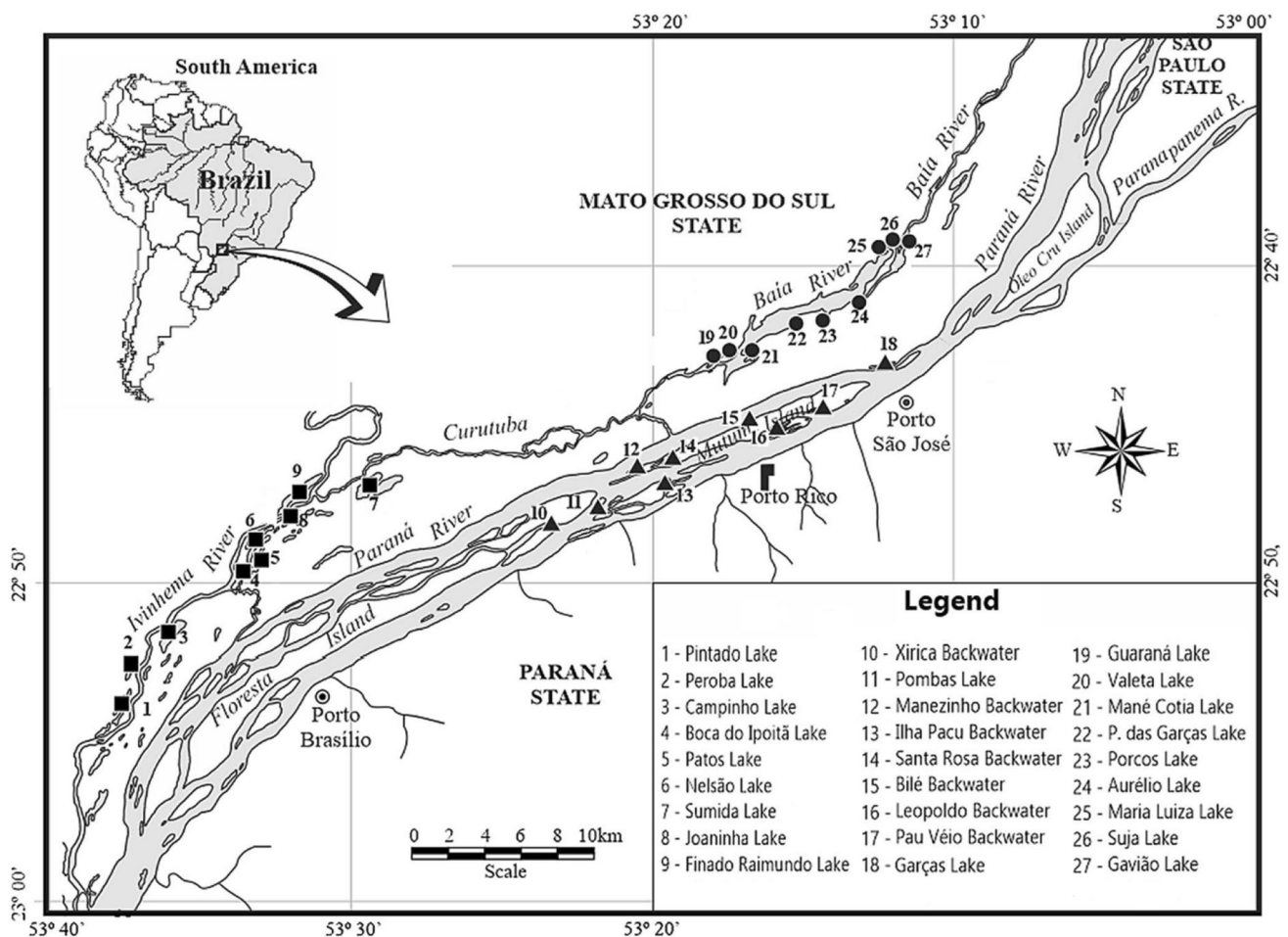
The Paraná River is the second largest river in South America (4695 km long), as well as the tenth largest river in the world in terms of water discharge and the fourth in drainage area ( $2.8 \times 10^6 \text{ km}^2$ ) (Agostinho et al. 2008). The Upper Paraná River includes approximately the first third of the Paraná River Basin with a drainage area of 891,000 km<sup>2</sup> or 10.5% of the total area of Brazil (Agostinho et al. 2008).

The present study was carried out in the Upper Paraná River floodplain, which is approximately 60 km long and 20 km wide, between Porto Primavera Dam and beginning of the Itaipu Reservoir. This floodplain comprises three systems of different rivers: Ivinhema, Paraná and Baía, each with peculiar abiotic characteristics (Souza-Filho 2009). In each system, nine lakes permanently connected

to the main rivers were selected for the present study (Fig. 1).

### Sampling and laboratory analysis

The sampling of ostracod communities associated with aquatic macrophytes was performed from January 31st to February 2nd, 2011 in 27 lakes of the Upper Paraná River floodplain. Ten aquatic macrophyte species were used in this study (see Table 1), and distributed over five types: (1) free-floating macrophytes: *Eichhornia crassipes* (Mart.), *Salvinia auriculata* Aubl., *Salvinia herzogii* (La Sota) Solms, *Salvinia minima* Baker and *Limnobium laevigatum* (HBK ex Willd.) Heine; (2) fixed macrophytes: *Nymphaea amazonum* Mart. Et Zucc.; (3) rooted macrophytes: *Eichhornia azurea* Kunth and *Hydrocotyle ranunculoides* L.; (4) free submerged macrophytes: *Utricularia foliosa* L.; (5) rooted submerged macrophytes: *Egeria najas* Planch. The richness of macrophytes was considered as the number of species of macrophytes found in each lake.



**Fig. 1** Location of the studied lakes of the Upper Paraná River floodplain. The symbols differentiate the systems: Ivinhema (squares 1–9), Paraná (triangles 10–18) and Baía (circles 19–27)

**Table 1** Geographic coordinates, types of system, species of macrophytes, and abiotic characteristics of the lakes for all samples

Locality name	System	Species of macrophytes	Coordinates	pH	EC ( $\mu\text{S cm}^{-1}$ )	DO ( $\text{mg L}^{-1}$ )	WT ( $^{\circ}\text{C}$ )	PE (km)	CO (km)	Ric
1. Pintado	Ivinhema	Ec, Sm	22°57'04.9"S 53°38'43.1"W	6.35	50.50	0.81	29.40	8.63	0.56941	2
2. Peroba	Ivinhema	Ec, Sm, Ea	22°54'39.4"S 53°38'34.5"W	6.19	48.20	0.15	29.10	2.26	0.08524	3
3. Campinho	Ivinhema	Ec, Hr, Sh, Ll	22°51'48.4"S 53°36'53.3"W	4.71	22.20	0.19	27.50	1.75	0.14781	4
4. Boca do Ipoitã	Ivinhema	Ec, Sa, Hr	22°50'08.1"S 53°33'58.5"W	6.09	44.80	0.14	30.70	0.74	0.00001	3
5. Patos	Ivinhema	Ec, Sm, Ea	22°49'0.53"S 53°33'20.3"W	5.93	42.80	0.14	30.20	20.09	1.37629	3
6. Nelsão	Ivinhema	Ec, Sm, Ea	22°49'32.5"S 53°33'50.8"W	6.14	42.30	0.62	31.10	1.53	0.00001	3
7. Sumida	Ivinhema	Ec, Ea, Hr, Sh	22°46'56.1"S 53°29'38.5"W	6.47	48.70	0.16	31.80	6.53	3.80358	4
8. Joanhina	Ivinhema	Uf, Ec	22°48'22.8"S 53°33'17.1"W	6.20	46.70	0.73	32.30	1.70	0.03780	2
9. Finado Raimundo	Ivinhema	Ec, Sm, Ea	22°47'48.6"S 53°32'11.6"W	6.43	49.20	2.54	31.10	7.98	0.12580	3
10. Xirica	Paraná	Ec, Ea	22°46'48.2"S 53°22'59.6"W	6.29	54.20	3.42	30.00	2.06	0.00001	2
11. Pombas	Paraná	Ec, Sm, Sh, Na	22°47'59.5"S 53°21'36.9"W	6.57	62.00	4.87	29.00	1.05	0.01183	4
12. Mazeninho	Paraná	Ec, Sm, Na	22°46'46.6"S 53°20'59.8"W	6.48	72.00	3.83	31.30	1.20	0.00001	3
13. Ilha Pacu	Paraná	Ec, Sh, Na	22°47'29.5"S 53°19'49.7"W	6.90	59.20	4.89	29.00	0.34	0.00001	3
14. Santa Rosa	Paraná	Ea, En, Sh, Ll	22°46'21.3"S 53°18'15.0"W	6.68	59.90	5.21	30.50	0.80	0.00001	4
15. Bilé	Paraná	Ec	22°45'13.7"S 53°17'0.6"W	6.42	80.90	2.15	33.70	2.28	0.00001	1
16. Leopoldo	Paraná	Ec, Sa	22°45'16.6"S 53°15'58.1"W	6.65	79.90	4.72	31.70	2.51	0.00001	2
17. Pau Véio	Paraná	Uf, Na, Ea	22°44'56.1"S 53°15'31.6"W	6.43	63.60	3.90	30.60	1.07	0.00001	3
18. Garças	Paraná	Ea, Sa	22°43'31.1"S 53°13'10.5"W	6.56	67.10	4.36	33.10	5.14	0.12634	2
19. Guaraná	Baía	Ec, Uf, Na, Sa, Ll, Hr	22°43'16.6"S 53°18'17.1"W	5.79	36.60	0.24	29.30	2.51	0.09630	6
20. Valeta	Baía	Ec, Uf	22°43'55.3"S 53°17'58.3"W	6.32	43.50	2.18	31.50	0.74	0.00001	2
21. Mané Cotia	Baía	Ll, Ec, Ea	22°43'16.4"S 53°17'0.5"W	5.95	43.70	0.40	30.50	1.85	0.00001	3
22. Pousada das Garças	Baía	Hr, Na	22°42'01.2"S 53°15'19.6"W	6.13	34.80	3.70	29.90	1.66	0.00001	2
23. Porcos	Baía	Sh, Ec, Hr	22°42'0.45"S 53°14'42.9"W	6.14	41.00	1.13	32.40	1.89	0.00001	3
24. Aurélio	Baía	Ea, Ec, Uf, Hr	22°41'37.7"S 53°13'54.3"W	5.95	43.80	0.53	31.60	1.34	0.00001	4
25. Maria Luiza	Baía	Ec, Uf, Ea, Ll	22°40'28.7"S 53°13'10.7"W	5.90	32.10	0.99	32.20	3.95	0.00001	4
26. Suja	Baía	Ec, Sh, Ea	22°40'0.02"S 53°12'46.6"W	5.54	26.70	1.83	31.60	3.10	1.07020	3
27. Gavião	Baía	Ec, Sh	22°40'52.1"S 53°12'58.0"W	5.66	23.20	2.45	31.20	0.63	0.00001	2

*Eichhornia crassipes* (Ec), *Salvinia auriculata* (Sa), *Salvinia herzogii* (Sh), *Salvinia minima* (Sm), *Nymphaea amazonum* (Na), *Eichhornia azurea* (Ea), *Hydrocotyle ranunculoides* (Hr), *Utricularia foliosa* (Uf), *Egeria najas* (En), Water temperature (WT), pH, electrical conductivity (EC), dissolved oxygen (DO), lake perimeter (PE), degree of connectivity (CO) and richness of macrophytes (Ric)

The aquatic macrophytes were removed manually from the water, transferred to a plastic bucket (Campos et al. 2017) and either the entire plants (in the case of *Salvinia* spp., *N. amazonum*, *U. foliosa*, *E. najas*) or only the roots (for *Eichhornia* spp., *L. laevigatum*, *H. ranunculoides*) were washed to remove the ostracods. The roots or whole plants were placed in plastic bags, dried and weighed in the lab to calculate ostracod densities (dividing the total number of organisms by the dry weight of the roots/whole plants). The material retained in the bucket was washed through a hand net with 160 µm mesh size and preserved in 70° ethanol buffered with sodium tetraborate.

Samples were divided with a Folsom fractionator and ¼ of the sample was quantified to estimate densities. However, the complete sample was used to estimate richness and abundance of species which were not recorded in the subsample. Ostracods were sorted using a stereoscopic microscope and were identified down to species level using specialized literature (see Martens and Behen 1994 and articles included therein; Rossetti and Martens 1998; Higuti et al. 2013; Higuti and Martens 2012a, b, 2014).

Several chemical and physical variables were measured *in situ*, such as pH and electrical conductivity ( $\mu\text{S cm}^{-1}$ ) (YSI 63), dissolved oxygen ( $\text{mg L}^{-1}$ ) and water temperature (°C) (YSI oximeter). The perimeter of the lakes (in km) and the estimation of the degree of connectivity (distance of the lake from the main river, in km) were obtained through the Google Earth® (2011) image program.

## Deconstructing the ostracods community

The biological traits considered were body size and locomotion mode. These traits were subdivided into five categories for the formation of the responses matrices:

1. body size: length (L) and height (H) of the ostracod carapace was measured using both scanning electron microscopy (SEM), and stereoscope microscope. Thus, species were categorized as small ( $L \leq 0.54$  mm and/or  $H \leq 0.32$  mm), medium ( $0.55 \leq L \leq 1.32$  mm and/or  $0.33 \leq H \leq 0.72$  mm) and large ( $L > 1.32$  mm and/or  $H > 0.72$  mm) (Matsuda et al. 2015);
2. locomotion mode: swimmers (with natatory setae on A2) and non-swimmers (without such setae or with these setae strongly reduced) (Meisch 2000).

## Data analysis

The environmental factors (abiotic and biotic variables) considered were: pH, electrical conductivity, dissolved oxygen, water temperature, perimeter of the lake, degree of connectivity and richness of aquatic macrophytes. These variables were log-transformed, except for pH and richness of macrophytes.

The spatial factors considered were derived from the matrix of the geographic coordinates of the sites, using the PCNM method (Principal Coordinates of Neighbor Matrices). The axes (eigenvectors) were used as spatial explanatory variables (Borcard and Legendre 2002). In this analysis, the first PCNMs selected represent larger scales of amplitude, whereas later PCNMs represent smaller scaling variations.

The relative importance of environmental and spatial factors on the metacommunity structure of ostracods was analysed using a partial redundancy analysis (pRDA), firstly using a density data matrix, with all species and subsequently using matrices with each category of biological traits. We used the ostracod density matrix (mean of the ostracod density of different species of macrophytes in each lake) of 27 sample units (lakes). These matrices were Hellinger transformed (Peres-Neto et al. 2006), which is an appropriate method for matrices comprising a large number of zeros (Legendre and Gallagher 2001). The variation of the ostracod community was partitioned into a purely environmental component (*E*), a purely spatial component (*S*), a component explained by environmental and spatial factors (*E∩S*) and finally the unexplained variation (*R*). The importance of fractions *E* and *S* were tested using 999 random permutations.

The environmental and spatial factors were selected through forward selection, in order to identify which are relevant to ostracods and which should be included in the analysis (Blanchet et al. 2008). The results were adjusted  $R^2$  values and the components were considered significant when  $p < 0.05$ .

Subsequently, multivariate non-metric multi-dimensional scaling (NMDS) was applied using ostracod density data, based on the Bray–Curtis similarity indexes, with the aim to rank the ostracod community structure according to each species of macrophytes found in the different lakes. The difference in ostracods composition amongst the species of macrophytes was tested using a permutational analysis of variance (PERMANOVA) to the similarity matrix, utilizing 999 permutations. Significant results of PERMANOVA were submitted to pair-wise comparisons to determine which plants were important in relation to ostracod species composition. Analyses were performed using statistical software R and Vegan package (R Core Team 2014). The figures were drawn using the program Statistica 7.1 (StatSoft Inc. 2005) and PowerPoint.

## Results

### Ostracod species composition and biological traits

We recorded 37 species of ostracods, belonging to four families: Cyprididae, Candonidae, Limnocytheridae and

**Table 2** Biological traits of the ostracods species associated with aquatic macrophytes

	<i>H</i> (mm)	<i>L</i> (mm)	Size	Locomotion mode
Family Cyprididae				
<i>Diaphanocypris meridana</i> (Furtos, 1936)	0.55	1.30	Medium	Swimmer
<i>Stenocypris major</i> Braid, 1985	0.65	1.59	Large	Swimmer
<i>Stenocypris malayica</i> Victor & Fernando, 1981	0.55	1.14	Large	Swimmer
<i>Strandesia psittacea</i> (Sars, 1901)	0.87	1.61	Medium	Swimmer
<i>Strandesia</i> cf. <i>psittacea</i> sp. 2	0.96	1.50	Large	Swimmer
<i>Strandesia mutica</i> (Sars, 1901)	0.75	1.46	Large	Swimmer
<i>Strandesia variegata</i> (Sars, 1901)	0.75	1.32	Large	Swimmer
<i>Strandesia tolimensis</i> Roessler, 1990	0.58	0.91	Medium	Swimmer
<i>Strandesia lansactohai</i> Higuti & Martens, 2013 (in Higuti et al. 2013)	0.51	0.97	Medium	Swimmer
<i>Strandesia velhoi</i> Higuti & Martens, 2013 (in Higuti et al. 2013)	0.68	1.14	Medium	Swimmer
<i>Strandesia nupelia</i> Higuti & Martens, 2013 (in Higuti et al. 2013)	0.61	1.04	Medium	Swimmer
<i>Strandesia</i> sp. 9 n.sp	0.57	1.15	Medium	Swimmer
<i>Strandesia</i> sp. 10 n.sp	0.38	0.96	Medium	Swimmer
<i>Bradleystrandesia trispinosa</i> (Pinto & Purper, 1965)	0.56	0.94	Medium	Swimmer
<i>Cabelodopsis hispida</i> (Sars, 1901)	0.53	0.89	Medium	Swimmer
<i>Bradleyriebella lineata</i> (Victor & Fernando, 1981)	0.32	0.62	Medium	Swimmer
<i>Cypricerus centrura</i> (Klie, 1940)	0.54	1.18	Medium	Swimmer
<i>Chlamydotheca deformis</i> (Farkas, 1958)	1.46	2.33	Large	Swimmer
<i>Chlamydotheca iheringi</i> (Sars, 1901)	2.04	3.21	Large	Swimmer
<i>Chlamydotheca</i> cf. <i>iheringi</i> sp. 2	1.84	2.96	Large	Swimmer
<i>Cyprretta costata</i> G. W. Muller, 1898	0.50	0.66	Medium	Swimmer
<i>Cyprretta</i> sp. 2 n.sp	0.28	0.40	Small	Swimmer
<i>Cypridopsis vidua</i> O.F. Müller, 1898	0.4	0.64	Medium	Swimmer
<i>Cypridopsis</i> cf. <i>vidua</i> sp. 2	0.32	0.53	Small	Swimmer
“ <i>Cypridopsis</i> ” sp. 1 n.gen. n.sp	0.28	0.51	Small	Swimmer
“ <i>Cypridopsis</i> ” sp. 2 n.gen. n.sp	0.17	0.38	Small	Swimmer
<i>Neocypridopsis nana</i> (Sars, 1901)	0.25	0.35	Small	Swimmer
Family Candonidae				
<i>Candobrasilopsis brasiliensis</i> Sars, 1901	0.49	0.97	Medium	Non-swimmer
<i>Candobrasilopsis rochai</i> Higuti & Martens, 2012	0.35	0.75	Medium	Non-swimmer
<i>Candobrasilopsis elongata</i> Higuti & Martens, 2014	0.44	0.99	Medium	Non-swimmer
<i>Pseudocandona agostinhoi</i> Higuti & Martens, 2014	0.33	0.66	Medium	Non-swimmer
<i>Pseudocandona cillisi</i> Higuti & Martens, 2014	0.38	0.67	Medium	Non-swimmer
<i>Physocypria</i> sp. 1 n.sp	0.38	0.53	Small	Swimmer
Family Limnocytheridae				
<i>Cytheridella ilosvayi</i> Daday, 1905	0.48	0.78	Medium	Non-swimmer
Family Darwinulidae				
<i>Alicenula serricaudata</i> (Klie, 1935)	0.21	0.52	Small	Non-swimmer
<i>Vestalenula pagliolii</i> (Pinto & Kozian, 1961)	0.22	0.48	Small	Non-swimmer
<i>Penthesilenula brasiliensis</i> (Pinto & Kozian, 1961)	0.21	0.45	Small	Non-swimmer

Height measurements (*H*) and carapace length (*L*), body size categories and locomotion mode

Darwinulidae (Table 2). According to the trait “body size”, 9 species were classified as small, 20 as medium and 8 as large. For the trait “locomotion”, 28 species were classified as swimmers and 9 as non-swimmers (Table 2).

### Environmental and spatial factors

The significant variables selected with the forward selection analysis were pH, water temperature, dissolved oxygen,

electrical conductivity and richness of macrophytes. In addition, regarding the spatial factor, 14 PCNMs (eigenvectors) were derived and those selected are summarized in Table 3.

The pRDA analysis showed a significant influence of the environmental factors for the community as a whole, for species with medium and large body sizes, and for both swimming and non-swimming ostracods. On the other hand, the spatial effect was significant only for the swimming and non-swimming categories (Table 3).

Regarding the relative contributions (the adjusted  $R^2$ ), for the community as a whole, the percentage of potential explanation was 4% for environmental and 2% for spatial factors (Fig. 2a). Similarly, environmental factors were more

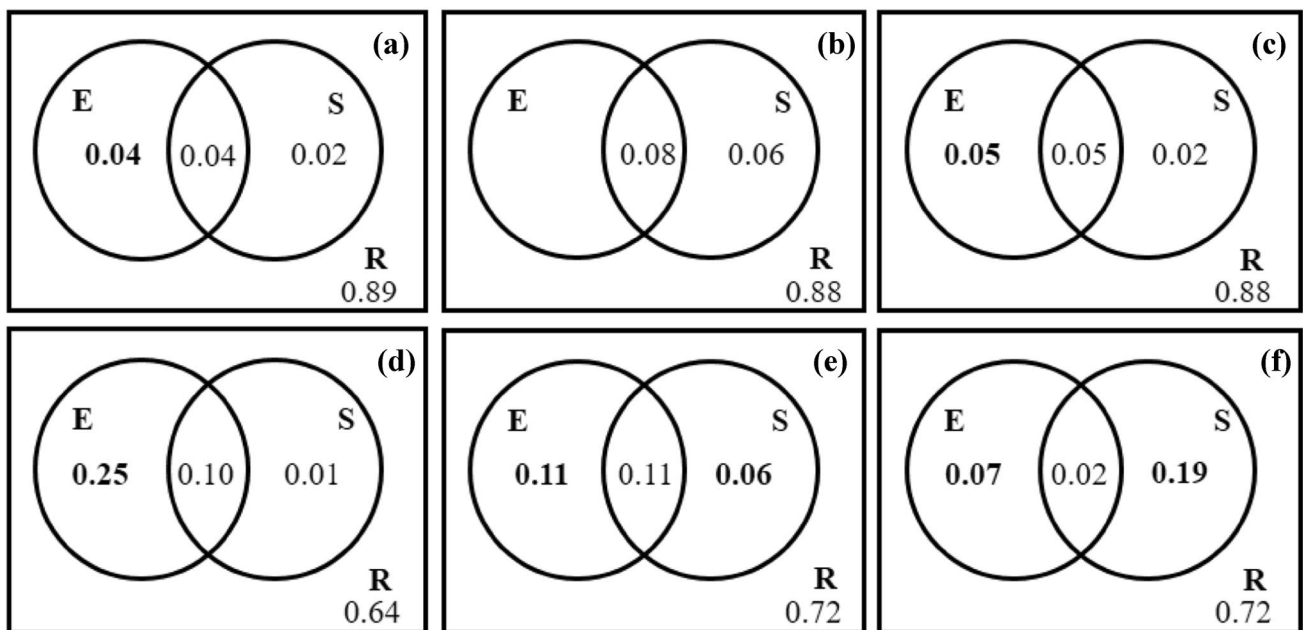
pronounced to medium (5%) and large-sized (25%) in relation to the spatial factor (2 and 1%, respectively) (Fig. 2c, d). Both environmental and spatial factors had low explanatory power for small-sized organisms (Fig. 2b). Environmental factors were more important for swimmers (11%) and spatial factors for non-swimmers (19%) (Fig. 2e, f). Furthermore, the distribution of small (8%) and large-sized (10%) and swimming organisms (11%) was attributed to the shared fraction of environmental and spatial factors.

The multivariate non-metric multi-dimensional scaling (NMDS) analysis showed distinct ostracod community structures according to the species of macrophytes, while some clustering was observed (Fig. 3), confirmed by

**Table 3** Results of the partial redundancy analysis (pRDA) for the ostracod community as a whole and deconstructed for the different biological traits

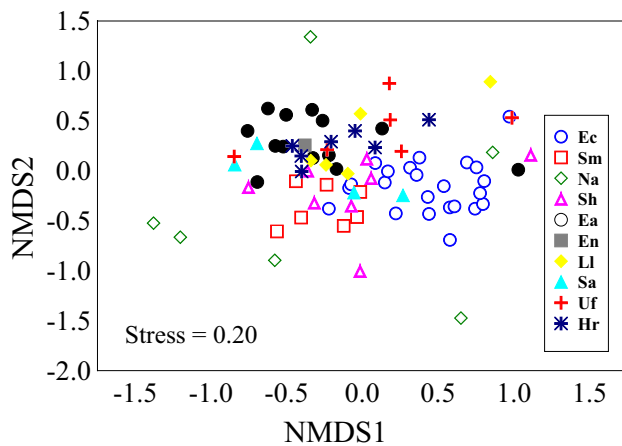
	Pure E		Pure S		Unexplained Adj. $R^2$	Selected variables	
	<i>P</i>	Adj. $R^2$	<i>P</i>	Adj. $R^2$		<i>E</i>	<i>S</i>
All taxa	<b>0.036</b>	0.04	0.164	0.02	0.89	DO	pcnm 1
Body size							
Small	0.671	-	0.073	0.06	0.88	pH	pcnm 2,6
Medium	<b>0.032</b>	0.05	0.140	0.02	0.88	DO	pcnm 1
Large	<b>0.028</b>	0.25	0.320	0.01	0.64	pH, EC	pcnm 9
Locomotion mode							
Swimmers	<b>0.046</b>	0.11	<b>0.039</b>	0.06	0.72	DO, WT, pH, Ric	pcnm 1,3
Non-swimmers	<b>0.001</b>	0.07	<b>0.001</b>	0.19	0.72	DO	pcnm 2,4

*P* significance level, *E* environmental factor, *S* spatial factor, *DO* dissolved oxygen, *WT* water temperature, *EC* electrical conductivity, *Ric* richness of macrophytes. Values in bold were significant  $P < 0.05$ . Values of the adjusted  $R^2 < 0$  have not been shown



**Fig. 2** Venn diagrams showing the relative contributions (% of explanation) of environmental (*E*), spatial (*S*) factors and unexplained fraction (*R*) of the community as a whole (a); small (b), medium (c) and

large (d) body size; swimmer (e) and non-swimmer (f) locomotion mode. Bold values were significant. Values  $< 0$  have not been shown



**Fig. 3** Multivariate analysis of Non-Metric Multi-Dimensional Scaling (NMDS) based on the density of ostracods in different species of macrophytes: *Eichhornia crassipes* (Ec), *Salvinia minima* (Sm), *Nymphaea amazonum* (Na), *Salvinia herzogii* (Sh), *Egeria najas* (En), *Limnium laevigatum* (Ll), *Utricularia foliosa* (Uf), *Eichhornia azurea* (Ea), *Salvinia auriculata* (Sa), *Hydrocotyle ranunculoides* (Hr)

PERMANOVA analysis (pseudo- $F=3.140$ ;  $p < 0.001$ ). The ostracod species composition associated with *Eichhornia crassipes* (Ec) was different from all other macrophyte species, except *Egeria najas* (En) (see all pair-wise comparisons in supplementary material Table S1).

## Discussion

Ostracod metacommunities as a whole, as well as the deconstructed metacommunities, were structured by distinct factors. However, a higher explanatory power of the environmental or spatial factors was observed for some categories of the biological traits, such as “large-sized”, as compared to the entire metacommunity. This is in agreement with the fact that the use of biological traits in metacommunity analyses captures environmental gradients more efficiently (Göthe et al. 2016) and consequently increases the explanatory power of the environmental or spatial factors. The analyses based on biological traits was thus useful to assess the structure of ostracod metacommunities, and comparable to other studies on aquatic macrophytes, macroinvertebrates and vertebrates (anurans and fish) (Landeiro et al. 2014; Silva and Hernández 2015; Göthe et al. 2016 respectively). However, Algarte et al. (2014) showed that deconstruction based on biological traits of periphytic algae was not relevant to the understanding of the mechanisms that drove this metacommunity, compared to the analysis of the community as a whole, as both were influenced by environmental factors. Thus, the usefulness of biological traits strongly depends on the biological group and on the approach considered. Göthe et al. (2016) compared traits composition vs. species

composition of aquatic macrophytes, macroinvertebrates and fish, and showed higher importance of environmental variation and trait composition than species composition. On the other hand, a study using species of aquatic insect, found that niche position was strongly related with the species distributions, whereas biological traits or taxonomic relatedness of species were less relevant (Heino and Mendoza 2016).

Natural systems present great variation in environmental and spatial processes at many temporal scales (Vanschoenwinkel et al. 2007) and studies have shown that for some organisms in subtropical freshwater systems, the factors that determine the metacommunities’ structure may change over time (Fernandes et al. 2014; Wojciechowski et al. 2017). In this way, snapshot surveys (a single sample in time) should be interpreted carefully. In floodplains, the hydrological pulses (either natural (local climate) or artificial (upstream reservoirs)) are the main factors responsible for changes in the biotic and abiotic characteristics of the environments (Junk and Sparks 1989). However, the ostracod community associated with aquatic macrophytes has been demonstrated to be temporally persistent over time during regular flood pulses, with deviations only occurring during extreme pulses, in the upper Paraná River floodplain (Higuti et al. 2007; Conçeição et al. 2018). Thus, owing to the temporal persistence of ostracod communities in the environments, we can infer that snapshot samples may truly represent the structure of ostracod metacommunities in this floodplain.

## Ostracod metacommunities as a whole

In the present study, the total ostracod metacommunity was influenced mainly by environmental factors. Thus, the species sorting mechanism seems to be important for the structuring of the community. This implies that the dispersal potential of the species in these communities was sufficient for them to occur only in environments with ecological characteristics that meet their requirements (Gonzalez 2009). Indeed, ostracods are generally excellent passive dispersers, as eggs, juveniles and adults can be carried by waterfowl, fish, plants and wind (Meisch 2000; Brochet et al. 2010; Pereira et al. 2017).

The explanatory power of the environmental and spatial factors was relatively low (11%) compared to other studies on ostracod metacommunities in lentic environments (Zhai et al. 2015; Castillo-Escrivà et al. 2016b, c). Therefore, other variables, not measured here, must be important as mentioned by Lindström and Langenheder (2012). For example, biological interactions and stochastic processes, as predicted by the neutral paradigm in metacommunity analyses, can also be responsible for the structuring of metacommunities (Chase 2007; Nabout et al. 2009).



## Metacommunities and biological traits

Several studies on aquatic communities (from invertebrate microorganisms to vertebrates) support the hypothesis that larger body sizes imply greater dispersal limitation (De Bie et al. 2012; Padial et al. 2014). However, our results contradict this pattern and one potential reason for this is that body size may interact with locomotion mode, so both of these features of organisms should be taken into account (see Heino et al., 2017). Here, we showed that all large-sized ostracods do have swimming behavior (see Table 2), and that it may be the latter characteristic that determines dispersal capacity, rather than size per sé. Likewise, De Bie et al. (2012) showed the importance of body size and locomotion mode, and demonstrated that small organisms, with efficient passive dispersal, were differently influenced by environmental and spatial factors, when compared to organisms with the same size, but with active dispersal.

In addition, the occurrence of small ostracods was poorly described by environmental and spatial factors. Therefore, other factors may affect presence or absence of this category of species. For example, presence or absence of predators, such as fish (Padial et al. 2009), can be highly relevant and determines to a large part the community structure of temporary pools, as well as of hypersaline lakes, in which at least vertebrate predators are absent (Martens et al. 2008).

With regard to locomotion mode, there was a difference in the influence of spatial factors between swimming and non-swimming ostracods. This means that locomotion mode is important for ostracod dispersal, for example, locally inside a lake. Furthermore, there was also a clearer interaction between mode of locomotion (swimming ostracods) and richness of macrophytes. Most likely, this was owing to the fact that at more local scales, higher diversity of macrophytes offers better opportunities for swimming ostracod species to select the optimal substrate. Non-swimming species must rely on stochastic processes to colonize optimal habitats.

Also, the shared fraction of environmental and spatial factors was important in structuring the ostracod metacommunities for some categories of biological traits (i.e. small and large-sized and swimmers). Some studies have shown similar results for ostracod metacommunities as a whole, with a shared influence of environmental and spatial factors (Escrivà et al. 2015; Castillo-Escrivà et al. 2016a, b). Therefore, existing species sorting mechanisms can be partially limited by dispersal, as was shown by Ng et al. (2009) and Lansac-Tôha et al. (2016).

## Selected environmental and spatial variables and importance of aquatic macrophytes

The selected abiotic variables are important to ostracods. For example, water temperature affects life history and body size

of these organisms (Aguilar-Alberola and Mesquita-Joanes 2014; Castillo-Escrivà et al. 2016a). Also, some lakes of the Upper Paraná River floodplain have large quantities of organic matter and the decomposition processes will deplete dissolved oxygen (Pagioro and Thomaz 1999). Finally, low pH will impede carapace calcification of ostracods (Higuti et al. 2010).

The selected spatial variables (PCNMs) confirmed that the distance amongst the environments was important for the structuring of the metacommunity. Thus, even with the reduced explanatory power of the variation (as compared to the environmental factor) and in spite of the fact that the range of the study area is relatively small (60 km long and 20 km wide), the spatial factor was still relevant in the structuring of the ostracod metacommunity (i.e. non-swimming ostracods). However, it must be emphasized that this ‘spatial-signal’ may be related to spatially structured abiotic or biotic variables that are here missing from the data (Heino et al. 2015).

The richness of macrophytes was important in the structuring of the swimming ostracod metacommunity. This is related to the strong association between ostracods and roots/plants, which serve as shelter, place of reproduction and foraging (Liberto et al. 2012). Similarly, Kiss (2004) found that species of aquatic macrophytes affects distribution and abundance of ostracods. Previous studies on ostracods in the Upper Paraná River floodplain have demonstrated the effects of aquatic macrophytes on diversity and abundance of ostracods. For example, Higuti et al. (2010) tested the influence of several ecological factors (habitat types, hydrological systems and substrates) on the variation of the ostracod community and demonstrated a greater effect of substrate type (sediment and aquatic macrophyte species), and strong association of several ostracods species with specific macrophytes, such as *Eichhornia crassipes* and *Pistia stratiotes*. Another recent study evaluated ostracod community composition on 10 species of aquatic macrophytes and observed a tendency for an association of ostracods, mainly of small size and non-swimming, with plants with more complex roots, such as *E. crassipes* (Matsuda et al. 2015). Our present results also show a different ostracod community composition according to macrophyte species and related fractal measurements (Matsuda et al. 2015), e.g., between *E. crassipes* (with greater structural complexity) and *E. azurea* (less complexity) (see Fig. 3).

## Summary

The present assessment based on community deconstruction was important for the analysis of the studied metacommunity of ostracods, because of the greater explanatory power of the environmental or spatial factors of some categories of

biological traits. Such results contribute to a better assessment of the structuring of metacommunities, when compared to results derived from analyses based on the community as a whole. The entire ostracod metacommunity and most of the organisms selected according to the biological traits seem to be influenced by the species sorting mechanism (mainly by environmental factors). In addition, the general pattern that larger body size necessarily decreases the possibilities for passive long-distance dispersal of the organisms was not corroborated here. Locomotion mode (swimming or non-swimming) was more important than size, because swimming ostracods may be better dispersers, especially at a more local scale. Thus, local variation in the composition of aquatic macrophyte communities in floodplain lakes has pronounced effect on ostracod community structuring.

**Acknowledgements** We thank Jaime Luiz Lopes Pereira (Maringá, Brazil) for the production of the map, Julien Cillis (Brussels, Belgium) provided technical assistance with the scanning electron microscopy (SEM) images used for the ostracod measurements. We thank the Ministry of Science and Technology (Ministério da Ciência e Tecnologia, MCT) and the National Council for Scientific and Technological Development (Conselho Nacional de Desenvolvimento Científico e Tecnológico, CNPq) for financial support (Edital Universal nr 476130/2010-7), coordinated by Dr Fábio Amodêo Lansac-Tôha, to whom we are also most grateful. We would like to thank the Nucleus of Research in Limnology, Ichthyology and Aquaculture (Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura, Nupélia) and the Post-graduate Program in the Ecology of Continental Aquatic Environments (Programa de Pós-Graduação em Ecologia de Ambientes Aquáticos Continentais, PEA) of the State University of Maringá (Universidade Estadual de Maringá, UEM) for continuous logistic support. RC, FMLT and EOC would like to thank the Coordination of Improvement of Higher Education Personnel (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, CAPES) and CNPq for granting their scholarships. The Universidade Estadual de Maringá, (UEM, Maringá) and the Royal Belgian Institute of natural Sciences (RBINS, Brussels) have a bilateral Memorandum of Understanding regarding collaborative Scientific Research. Two anonymous referees suggested important improvements.

## References

- Agostinho AA, Gomes LC, Thomaz SM, Hahn NS (2004) The upper Paraná River and its floodplain: main characteristics and perspectives for management and conservation. In: Thomaz SM, Agostinho AA, Hahn NS (eds) *The Upper Paraná river and its floodplain: physical aspects, ecology and conservation*. Backhuys Publishers, Leiden, pp 381–393
- Agostinho AA, Pelicice FM, Gomes LC (2008) Dams and the fish fauna of the Neotropical region: impacts and management related to diversity and fisheries. *Braz J Biol* 68:1119–1132. <https://doi.org/10.1590/S1519-69842008000500019>
- Aguiar-Alberola JA, Mesquita-Joanes F (2014) Breaking the temperature-size rule: thermal effects on growth, development and fecundity of a crustacean from temporary waters. *J Therm Biol* 42:15–24. <https://doi.org/10.1016/j.jtherbio.2014.02.016>
- Alahuhta J, Johnson LB, Olker J, Heino J (2014) Species sorting determines variation in the community composition of common and rare macrophytes at various spatial extents. *Ecol Complex* 20:61–68. <https://doi.org/10.1016/j.ecocom.2014.08.003>
- Algarde VM, Rodrigues L, Landeiro VL, Siqueira T, Bini LM (2014) Variance partitioning of deconstructed periphyton communities: does the use of biological traits matter? *Hydrobiologia* 722:279–290. <https://doi.org/10.1007/s10750-013-1711-6>
- Astorga A, Oksanen J, Luoto M, Soininen J, Virtanen R, Muotka T (2012) Distance decay of similarity in freshwater communities: do macro- and microorganisms follow the same rules? *Glob Ecol Biogeogr* 21:365–375. <https://doi.org/10.1111/j.1466-8238.2011.00681.x>
- Blanchet G, Legendre P, Borcard D (2008) Forward selection of spatial explanatory variables. *Ecology* 89:2623–2632. <https://doi.org/10.1890/07-0986.1>
- Borcard D, Legendre P (2002) All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecol Model* 153:51–68. [https://doi.org/10.1016/S0304-3800\(01\)00501-4](https://doi.org/10.1016/S0304-3800(01)00501-4)
- Brochet AL, Gauthier-Clerc M, Guillemain M, Fritz H, Waterkeyn A, Baltanás Á, Green AJ (2010) Field evidence of dispersal of branchiopods, ostracods and bryozoans by teal (*Anas crecca*) in the Camargue (southern France). *Hydrobiologia* 637:255–261. <https://doi.org/10.1007/s10750-009-9975-6>
- Campos R, Conceição EO, Pinto MBO, Bertoin APS, Higuti J, Martens K (2017) Evaluation of quantitative sampling methods in pleuston: an example from ostracod communities. *Limnol Ecol Manag Int Waters* 63:36–41. <https://doi.org/10.1016/j.limno.2017.01.002>
- Castillo-Escrivà A, Rueda J, Zamora L, Hernández R, Del Moral M, Mesquita-Joanes F (2016a) The role of watercourse versus overland dispersal and niche effects on ostracod distribution in Mediterranean streams (eastern Iberian Peninsula). *Acta Oecol* 73:1–9. <https://doi.org/10.1016/j.actao.2016.02.001>
- Castillo-Escrivà A, Valls L, Rochera C, Camacho A, Mesquita-Joanes F (2016b) Disentangling environmental, spatial, and historical effects on ostracod communities in shallow lakes. *Hydrobiologia* 1–12. <https://doi.org/10.1007/s10750-016-2945-x>
- Castillo-Escrivà A, Valls L, Rochera C, Camacho A, Mesquita-Joanes F (2016c) Spatial and environmental analysis of an ostracod metacommunity from endorheic lakes. *Aquat Sci* 78:707–716. <https://doi.org/10.1007/s00027-015-0462-z>
- Castillo-Escrivà A, Valls L, Rochera C, Camacho A, Mesquita-Joanes F (2017) Metacommunity dynamics of Ostracoda in temporary lakes: Overall strong niche effects except at the onset of the flooding period. *Limnol Ecol Manag Int Waters* 62:104–110. <https://doi.org/10.1016/j.limno.2016.11.005>
- Chase JM (2007) Drought mediates the importance of stochastic community assembly. *Proc Natl Acad Sci* 104:17430–17434. <https://doi.org/10.1073/pnas.0704350104>
- Conceição EO, Higuti J, Campos R, Martens K (2018) Effects of flood pulses on persistence and variability of pleuston communities in a tropical floodplain lake. *Hydrobiologia* 807:175–188. <https://doi.org/10.1007/s10750-017-3392-z>
- De Bie T, De Meester L, Brendonck L, Martens K, Goddeeris B, Ercken D, Hampel H, Denys L, Vanhecke L, Van der Gucht K, Van Wichelen J, Vyverman W, Declerck SAJ (2012) Body size and dispersal mode as key traits determining metacommunity structure of aquatic organisms. *Ecol Lett* 15:740–747. <https://doi.org/10.1111/j.1461-0248.2012.01794.x>
- Escrivà A, Poquet J, Mesquita-Joanes F (2015) Effects of environmental and spatial variables on lotic ostracod metacommunity structure in the Iberian Peninsula. *Int Waters* 5:283–294. <https://doi.org/10.5268/IW-5.3.771>
- Fernandes IM, Henriques-Silva R, Penha J, Zuanon J, Peres-Neto PR (2014) Spatiotemporal dynamics in a seasonal metacommunity structure is predictable: the case of floodplain-fish

- communities. *Ecography* 37(5):464–475. <https://doi.org/10.1111/j.1600-0587.2013.00527.x>
- Gonzalez A (2009) Metacommunities: spatial community ecology. *Encycl Life Sci*. <https://doi.org/10.1002/9780470015902.a0021230>
- Göthe E, Baattrup-Pedersen A, Wiberg-Larsen P, Graeber D, Kristensen EA, Friberg N (2016) Environmental and spatial controls of taxonomic versus trait composition of stream biota. *Freshw Biol* 62:397–413. <https://doi.org/10.1111/fwb.12875>
- Gravel D, Canham CD, Beaudet M, Messier C (2006) Reconciling niche and neutrality: the continuum hypothesis. *Ecol Lett* 9:399–409. <https://doi.org/10.1111/j.1461-0248.2006.00884.x>
- Gronroos M, Heino J, Siqueira T, Landeiro VL, Kotanen J, Bini LM (2013) Metacommunity structuring in stream networks: roles of dispersal mode, distance type, and regional environmental context. *Ecol Evol* 3:4473–4487. <https://doi.org/10.1002/ece3.834>
- Hájek M, Roleček J, Cottenie K, Kintrová K, Horsák M, Poulicková A, Hájková P, Fránková M, Díte D (2011) Environmental and spatial controls of biotic assemblages in a discrete semi-terrestrial *habitat*: comparison of organisms with different dispersal abilities sampled in the same plots. *J Biogeogr* 38:1683–1693. <https://doi.org/10.1111/j.1365-2699.2011.02503.x>
- Heino J (2011) A macroecological perspective of diversity patterns in the freshwater realm. *Freshw Biol* 56:1703–1722. <https://doi.org/10.1111/j.1365-2427.2011.02610.x>
- Heino J, Mendoza G (2016) Predictability of stream insect distributions is dependent on niche position, but not on biological traits or taxonomic relatedness of species. *Ecography* 39:1216–1226. <https://doi.org/10.1111/ecog.02034>
- Heino J, Melo AS, Siqueira T, Soininen J, Valanko S, Bini LM (2015) Metacommunity organisation, spatial extent and dispersal in aquatic systems: patterns, processes and prospects. *Freshw Biol* 60:845–869. <https://doi.org/10.1111/fwb.12533>
- Heino J, Alahuhta J, Ala-Hulkko T, Antikainen H, Bini LM, Bonada N, Detry T, Erős T, Hjort J, Kotavaara O, Melo AS, Soininen J (2017) Integrating dispersal proxies in ecological and environmental research in the freshwater realm. *Environ Rev* 25:334–349. <https://doi.org/10.1139/er-2016-0110>
- Higuti J, Martens K (2012a) Description of a new genus and species of Candonopsini (Crustacea, Ostracoda, Candoninae) from the alluvial valley of the Upper Paraná River (Brazil, South America). *Eur J Taxon*:1–31
- Higuti J, Martens K (2012b) On a new cypridopsine genus (Crustacea, Ostracoda, Cyprididae) from the Upper Paraná River Floodplain (Brazil). *Zootaxa* 38:23–38
- Higuti J, Martens K (2014) Five new species of Candoninae (Crustacea, Ostracoda) from the alluvial valley of the Upper Paraná River (Brazil, South America). *Eur J Taxon* 106:1–36. <https://doi.org/10.5852/ejt.2014.106>
- Higuti J, Martens K (2016) Invasive South American floating plants are a successful substrate for native Central African pleuston. *Biol Invasion* 18:1191–1201. <https://doi.org/10.1007/s10530-016-1061-1>
- Higuti J, Velho LFM, Lansac-Tôha FA, Martens K (2007) Pleuston communities are buffered from regional flood pulses: the example of ostracods in the Paraná River floodplain, Brazil. *Freshw Biol* 52:1930–1943. <https://doi.org/10.1111/j.1365-2427.2007.01821.x>
- Higuti J, Declerck SAJ, Lansac-Tôha FA, Velho LFM, Martens K (2010) Variation in ostracod (Crustacea, Ostracoda) communities in the alluvial valley of the upper Paraná river (Brazil) in relation to substrate. *Hydrobiologia* 644:261–278. <https://doi.org/10.1007/s10750-010-0122-1>
- Higuti J, Schön I, Audenaert L, Martens K (2013) On the *Strandesia obtusata/elliptica* lineage (Ostracoda, Cyprididae) in the alluvial valley of the upper Paraná river (Brazil), with the description of three new species. *Crustaceana* 86:182–211. <https://doi.org/10.1163/15685403-00003160>
- Hoeinghaus DJ, Winemiller KO, Birnbaum JS (2007) Local and regional determinants of stream fish assemblage structure: Inferences based on taxonomic vs. functional groups. *J Biogeogr* 34:324–338. <https://doi.org/10.1111/j.1365-2699.2006.01587.x>
- Hubbell SP (2001) The unified neutral theory of biodiversity and biogeography. *Ecology* 32:1771–1772
- Junk WJ, Sparks RE (1989) The flood pulse concept in river-floodplain systems. *Can J Fish Aquat Sci* 106:110–127. <https://doi.org/10.1127/lr/11/1999/261>
- Kiss A (2007) Factors affecting spatial and temporal distribution of Ostracoda assemblages in different macrophyte habitats of a shallow lake (Lake Fehér, Hungary). *Hydrobiologia* 585:89–98. <https://doi.org/10.1007/s10750-007-0631-8>
- Landeiro VL, Waldez F, Menin M (2014) Spatial and environmental patterns of Amazonian anurans: Differences between assemblages with aquatic and terrestrial reproduction, and implications for conservation management. *Nat Conserv Braz J Nat Conserv* 12:42–46. <https://doi.org/10.4322/natcon.2014.008>
- Lansac-Tôha FM, Meira BR, Segovia BT, Lansac-Tôha FA, Velho LFM (2016) Hydrological connectivity determining metacommunity structure of planktonic heterotrophic flagellates. *Hydrobiologia* 781:81–94. <https://doi.org/10.1007/s10750-016-2824-5>
- Legendre P, Gallagher ED (2001) Ecologically meaningful transformations for ordination of species data. *Oecologia* 129:271–280. <https://doi.org/10.1007/s004420100716>
- Leibold MA, Holyoak M, Mouquet N, Amarasekare P, Chase JM, Hoopes MF, Holt RD, Shurin JB, Law R, Tilman D, Loreau M, Gonzalez A (2004) The metacommunity concept: a framework for multi-scale community ecology. *Ecol Lett* 601–613. <https://doi.org/10.1111/j.1461-0248.2004.00608.x>
- Liberto R, Mesquita-Joanes F, César I (2012) Dynamics of pleustonic ostracod populations in small ponds on the Island of Martín García (Rio de la Plata, Argentina). *Hydrobiologia* 688:47–61. <https://doi.org/10.1007/s10750-011-0600-0>
- Lindström ES, Langenheder S (2012) Local and regional factors influencing bacterial community assembly. *Environ Microbiol Rep* 4:1–9. <https://doi.org/10.1111/j.1758-2229.2011.00257.x>
- Logue JB, Mouquet N, Peter H, Hillebrand H (2011) Empirical approaches to metacommunities: a review and comparison with theory. *Trends Ecol Evol* 26:482–491. <https://doi.org/10.1016/j.tree.2011.04.009>
- Martens K, Behen F (1994) A checklist of the recent non-marine ostracods (Crustacea, Ostracoda) from the inland waters of South America and adjacent islands. *Trav Sci Du Mus Natl D'Histoire Nat Luxemb* 22:1–81
- Martens K, Schön I, Meisch C, Horne DJ (2008) Global diversity of ostracods (Ostracoda, Crustacea) in freshwater. *Hydrobiologia* 595:185–193. <https://doi.org/10.1007/s10750-007-9245-4>
- Matsuda JT, Lansac-Tôha FA, Martens K, Velho LFM, Mormul RP, Higuti J (2015) Association of body size and behavior of freshwater ostracods (Crustacea, Ostracoda) with aquatic macrophytes. *Aquat Ecol* 49:321–331. <https://doi.org/10.1007/s10452-015-9527-2>
- Meisch C (2000) Freshwater ostracoda of Western and Central Europe. In: Schwoerber J, Zwick P (eds) *Sußwasserfauna von Mitteleuropa* 8/3. Spektrum Akademischer Verlag, Heidelberg, p 522
- Nabout C, Siqueira T, Bini LM, Nogueira IDS (2009) No evidence for environmental and spatial processes in structuring phytoplankton communities. *Acta Oecol*. <https://doi.org/10.1016/j.actao.2009.07.002>
- Ng ISY, Carr CM, Cottenie K (2009) Hierarchical zooplankton metacommunities: distinguishing between high and limiting dispersal mechanisms. *Hydrobiologia* 619:133–143. <https://doi.org/10.1007/s10750-008-9605-8>

- Padial A, Thomaz SM, Agostinho AA (2009) Effects of structural heterogeneity provided by the floating macrophyte *Eichhornia azurea* on the predation efficiency and habitat use of the small Neotropical fish *Moenkhausia sanctaefilomenae*. *Hydrobiologia* 624:161–170. <https://doi.org/10.1007/s10750-008-9690-8>
- Padial A, Ceschin F, Declerck SAJ, De Meester L, Bonecker CC, Lansac-Tôha FA, Rodrigues L, Rodrigues LC, Train S, Velho LFM, Bini LM (2014) Dispersal ability determines the role of environmental, spatial and temporal drivers of metacommunity structure. *PLoS One* 9:1–8. <https://doi.org/10.1371/journal.pone.0111227>
- Pagioro TA, Thomaz SM (1999) Influence of the decomposition of *Eichhornia azurea* on selected abiotic limnological variables of different environments of the floodplain of the Paraná River. *Acta Limnol Bras* 11:157–171
- Pandit SN, Kolasa J, Cottenie K, Kolasa J (2009) Contrasts between habitat generalists and specialists: an empirical extension to the basic metacommunity framework. *Ecology* 90:2253–2262. <https://doi.org/10.1890/08-0851.1>
- Pereira LC, Lansac-Tôha FA, Martens K, Higuti J (2017) Biodiversity of ostracod communities (Crustacea, Ostracoda) in a tropical floodplain. *Inland Waters* 7(3):323–332. <https://doi.org/10.1080/20442041.2017.1329913>
- Peres-Neto PR, Legendre P, Dray S, Borcard D (2006) Variation partitioning of species data matrices: estimation and comparison of fractions. *Ecology* 87:2614–2625. [https://doi.org/10.1890/0012-9658\(2006\)87\[2614:VPOSDM\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[2614:VPOSDM]2.0.CO;2)
- Petsch DK, Pinha GD, Dias JD, Takeda AM (2015) Temporal nestedness in Chironomidae and the importance of environmental and spatial factors in species rarity. *Hydrobiologia* 745:181–193. <https://doi.org/10.1007/s10750-014-2105-0>
- R Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. <http://www.R-project.org>
- Ricklefs RE (1987) Community diversity: relative roles of and regional processes. *Science* 235:167–171. <https://doi.org/10.1126/science.235.4785.167>
- Rossetti G, Martens K (1998) Taxonomic revision of the recent and Holocene representatives of the family Darwinulidae (Crustacea, Ostracoda), with a description of three new genera. *Bull l'Institut R des Sci Nat Belgique Sci la Terre* 68:55–110
- Silva PG, Hernández MIM (2015) Scale-dependence of processes structuring dung beetle metacommunities using functional diversity and community deconstruction approaches. *PLoS One* 10:1–29. <https://doi.org/10.1371/journal.pone.0123030>
- Siqueira T, Bini LM, Roque FO, Couceiro SRM, Trivinho-Strixino S, Cottenie K (2011) Common and rare species respond to similar niche processes in macroinvertebrate metacommunities. *Ecography* 1–10. <https://doi.org/10.1111/j.1600-0587.2011.06875.x>
- Souza Filho EE (2009) Evaluation of the Upper Paraná River discharge controlled by reservoirs. *Braz J Biol* 69:707–716. <https://doi.org/10.1590/S1519-69842009000300024>
- StatSoft Inc (2005). STATISTICA (data analysis software system) version 7.1. [www.statsoft.com](http://www.statsoft.com)
- Thomaz SM, Cunha ER (2010) The role of macrophytes in habitat structuring in aquatic ecosystems: methods of measurement, causes and consequences on animal assemblages' composition and biodiversity. *Acta Limnol Bras* 22:218–236. <https://doi.org/10.4322/actalb.02202011>
- Vanschoenwinkel B, De Vries C, Seaman M, Brendonck L (2007) The role of metacommunity processes in shaping invertebrate rock pool communities along a dispersal gradient. *Oikos* 116(8):1255–1266. <https://doi.org/10.1111/j.0030-1299.2007.15860.x>
- Wiegandner AK, Jones BK, Ng ISY, Siqueira T, Cottenie K (2012) The terminology of metacommunity ecology. *Trends Ecol Evol* 27:253–254. <https://doi.org/10.1016/j.tree.2012.01.007>
- Wojciechowski J, Heino J, Bini LM, Padial AA (2017) The strength of species sorting of phytoplankton communities is temporally variable in subtropical reservoirs. *Hydrobiologia* 800:31–43. <https://doi.org/10.1007/s10750-017-3245-9>
- Zhai M, Nováček O, Výravský D, Syrovátka V, Bojková J, Helesic J (2015) Environmental and spatial control of ostracod assemblages in the Western Carpathian spring fens. *Hydrobiologia* 745:225–239. <https://doi.org/10.1007/s10750-014-2104-1>