



# Effects of flood pulses on persistence and variability of pleuston communities in a tropical floodplain lake

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**Abstract** Large rivers in tropical regions can experience strong variations of abiotic factors owing to the occurrence of flood pulses. Both man-made and natural floods can cause pulses with varying intensity and duration. Here, we test the hypothesis that ostracod communities in the pleuston of floating plants are persistent during regular pulses and more variable during extreme floods. Ostracod communities were monitored in the Manezinho Backwater of the Upper Paraná River floodplain (Brazil) for 83 months

(seven hydrologic cycles). Flood pulses directly influenced the abiotic variables, which in turn were correlated with the species composition and abundance of ostracods. Variability in the species composition differentiated only between the limnophase of cycle 4 (L4: 2009) and the subsequent extreme flood of cycle 5 (P5: 2009–2010). The longer duration and higher intensity of the extreme flood can increase the exchange of organisms through the aquatic connections between the lake and the river and can potentially trigger the hatching of dry-resistant eggs, increasing variability in ostracod species composition. The absence of significant differences in the species composition variability between the other succeeding periods shows that these communities are persistent

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and buffered to the effects of natural pulses of short durations.

**Keywords** Ostracoda · Microcrustaceans · Aquatic macrophytes · El Niño · Extreme flood events

## Introduction

Hydrological (flood) pulses can cause important environmental variations in floodplain systems. Floods can be the main controller of the abiotic factors, which subsequently influence the species composition. Species developed life history strategies that allow their persistence in disturbance regime due to seasonality of the pulses (Bunn & Arthington, 2002). Besides, the flood increases the connectivity between the aquatic environments that allows the recruitment of new individuals in populations, but also facilitates the colonization of species that potentially can change the dynamics of the communities, making them more variable (Bunn & Arthington, 2002).

Neiff (1990) defines two phases in flooding cycles: potamophases (flood periods) during which horizontal flows of living organisms, debris and sediments are pushed sideways from the riverbed towards laterally situated lakes and channels, and limnophases (drought periods) during which these elements are drained back toward the main riverbed. These well-defined periods cause changes in patterns of distribution and species abundance of floodplain lake communities (Junk & Sparks, 1989; Thomaz et al., 2007). In addition to regular, moderate pulses, more irregular and larger flood pulses can also occur. In the Upper Paraná River Floodplain, for example, such extreme floods occur on average once a year (Thomaz et al., 2004). Floodplains are therefore convenient aquatic systems to study causes and consequences of variability in community structure.

High floods, and even more so extreme floods, will homogenize floodplain biodiversity through increased habitat similarity, which in turn is (in part) owing to decreased variation in limnological factors (Thomaz et al., 2007). During periods of low water levels, the landscape will become more heterogeneous through increased isolation of habitats. This will result in an increase of variability in the species composition amongst the different habitats (Bozelli et al., 2015).

The natural dynamics of flood pulses in floodplains has been strongly influenced by the construction of man-made dams. In such dams, water release to downstream habitats is controlled by man and results in irregular floods downstream of such reservoirs (Souza Filho, 2009).

Another, more natural, factor that causes interannual variations in seasonal fluctuations in the flood levels is the precipitation variation caused by the El Niño-Southern Oscillation phenomenon. The alternating El Niño and La Niña episodes are caused by anomalous warming and cooling of the waters of the Central and East Equatorial Pacific Ocean and can in addition be intensified or weakened by the difference in atmospheric pressure between the Central and West Pacific, the so-called South Oscillation index (SO; Cera & Ferraz, 2015). Occurrences of El Niño of greater amplitude can cause extreme floods around the world (Ward et al., 1999, 2014). In Brazil, for example, this phenomenon can cause intense drought in the north and higher precipitation in the south during the summer season (Cera & Ferraz, 2015).

Effects of limnophases and potamophases have already been studied in several aquatic communities. Cichlid assemblages are persistence during interannual variations of water level, showing two equilibrium points, one in the early limnophase and the other in the early potamophase (Lourenço et al., 2012). Phytoplankton species richness and abundance are more variable in periods of normal floods due to environmental fluctuations. On the other hand, in extreme limnophases (drought) these communities are persistence and less variable (Bortolini et al., 2016). The limnophase increase temporal dissimilarity of zooplankton community, whereas the potamophase maintains a lower variability of environmental characteristics, sustaining a lower temporal variability of the community (Simões et al., 2013). The effects of fluctuation in water level on macroinvertebrates are more often studied in streams. In general, macroinvertebrate communities show greater persistence in cases where flow conditions remained relatively constant (Scarsbrook, 2002; Collier, 2008).

Pleuston communities, however, have thus far rarely been investigated. Higuti et al. (2007) postulated that the origin of pleuston in general, and its associated communities, e.g., ostracods, might be an adaptation to buffer the limiting effects of flood pulses. Indeed, extreme flood pulses, causing for

example an increase in water level of 6 m or more overnight, might cause sediments to become anoxic. This is a danger for obligate benthic communities, but pleuston in root systems of floating plants, typical of South American floodplains, will not be impacted as these plants simply follow the rising water levels. Given that ostracods can abound in pleuston (Higuti & Martens, 2016), they are an excellent model system to study effects of flood pulses on community structure.

Here, we investigate the effects of flood pulses on the variability of the species composition in ostracod communities over seven hydrological cycles (potamophase and limnophase periods). We analyze the variability over subsequent periods (P1, L1, P2, L2, ..., P7, L7) and between interperiods (non-subsequent periods—Fig. 1). We test the hypothesis that ostracod communities are largely persistent during regular pulses and are more variable during extreme floods. We expected that: (i) variation in abiotic factors will occur as a result of the oscillation of the flood pulses and will in its turn influence the ostracod community structure, (ii) the variability of the ostracod species composition will increase over time after a potamophase (high flood levels) and (iii) more environmentally tolerant species will occur in potamophase periods, as compared to in limnophase periods.

## Materials and methods

### Study area

The Upper Paraná River Floodplain (c 230 km long and c 20 km wide) has a hydrological regime consisting of flood pulses, alternating with periods of low water levels (Junk & Sparks, 1989). This floodplain is the last dam-free stretch of the entire Paraná River, where the 25 man-made reservoirs located into its

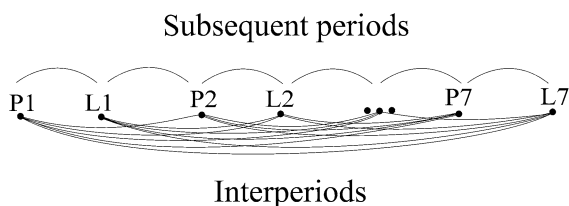
basin affect 70% of the total length of the river. The floodplain includes areas that are vital to biodiversity conservation (Ward et al., 1999; Agostinho et al., 2000). The intensity of extreme precipitation events, such as El Niño episodes, in southeastern South America has had significant impacts on the Paraná River flow rate (Grimm & Tedeschi, 2009).

One lentic backwater, named Manezinho, was monitored in the Upper Paraná River Floodplain for 7 years (from 2004 to 2005 and from 2007 to 2013). It is permanently connected to the main Paraná River by a narrow channel of 1 m long and 3 m wide. The backwater is located on the right bank of the Mutum Island and has a length of approximately 100 m, an area of c 0.1 ha, a perimeter of 2,330 m, and a mean depth of 2.1 m (Edvard et al., 2000). Samples were collected in three patches of *Eichhornia crassipes* (Mart.) Solms (considered as replicates in this study), along the backwater with station S1 situated furthest in the backwater, S2 in the center and S3 situated close to the entrance of the backwater (Fig. 2).

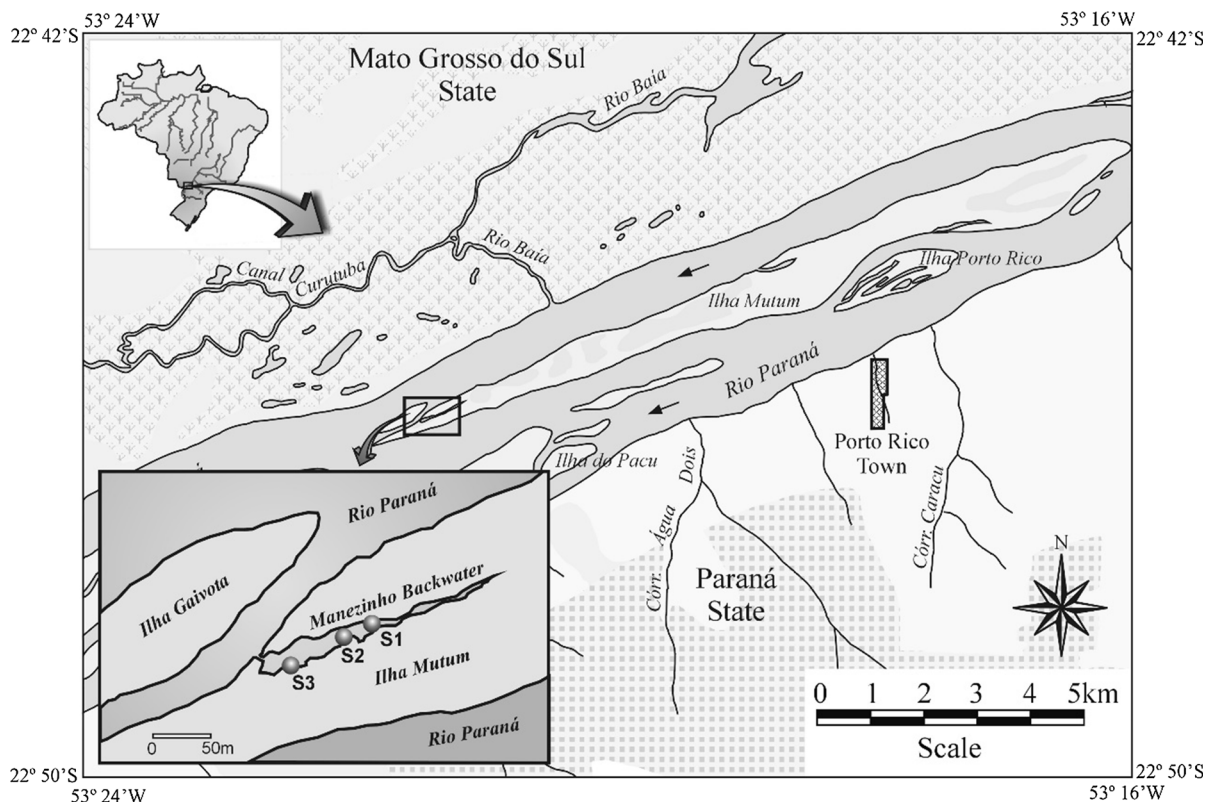
### Sampling, sorting, and identification of ostracods

Samples were taken monthly, from March 2004 to January 2005 and from February 2007 to February 2013 in Manezinho Backwater, totalling 83 months of sampling. From each macrophyte stand (S1–3), three individual *E. crassipes* plants were transferred to a plastic bucket (Campos et al., 2017). The roots of *E. crassipes* were separated and washed in the bucket to remove the ostracods, and the aerial part of the plant was discarded. The washed roots were placed in plastic bags and later were dried and weighed. The material resulting from washing was filtered through a hand net with 160  $\mu\text{m}$  mesh size, and the samples were preserved in 70° ethanol buffered with sodium tetraborate.

The physical and chemical variables of the water were measured in situ before the collection of ostracods. The water temperature (WT, °C) and dissolved oxygen (DO,  $\text{mg l}^{-1}$ ) were measured by YSI 550A oximeter, pH and electrical conductivity (EC,  $\mu\text{S cm}^{-1}$ ) using the YSI Model 63 apparatus. Water level data were obtained by the Long-Term Ecological Research project (site 6—[http://www.peld.uem.br/peld-nivel\\_fluviometrico.htm](http://www.peld.uem.br/peld-nivel_fluviometrico.htm)) of the Nucleus of Research in Limnology, Ichthyology and



**Fig. 1** Illustration to visualize the concept of subsequent period and interperiod comparisons



**Fig. 2** Location of the sampling stations (S1–3) in the Manezinho Backwater, in the Upper Paraná River Floodplain

Aquaculture (Nupélia) from the State University of Maringá (UEM).

In the laboratory, the samples were divided using a Folsom fractioner, 1/4 of the sample was used for quantification of ostracods, while the entire sample was used to quantify species richness. We used a Gehaka BK 3000 semi-analytical balance to weigh the roots of *E. crassipes*. Ostracods were sorted using a stereoscopic microscope and were identified down to species level using specialized literature (see Martens & Behen, 1994 and articles included; Rossetti & Martens, 1998; Higuti & Martens, 2012a, b, 2014; Higuti et al., 2013). The density of ostracods was calculated and estimated in relation to the dry weight of *E. crassipes* roots (ind  $g^{-1}$  DW).

#### Classification of data

The water level data were classified according to the hydrological cycles, limnophases (drought periods), and potamophases (flood periods), to facilitate inter-annual comparisons. For the selection of the periods,

we considered both the starting month and the month that marked its end (Table 1). The reference water level of the Paraná River of 350 cm (Souza Filho, 2009) was used to classify the limit between the two hydrological periods: limnophase  $<350$  cm and potamophase  $\geq 350$  cm.

#### Data analysis

The limnophase amplitude (number of days represented by the water level  $<350$  cm) and potamophase amplitude (number of days represented by the water level  $\geq 350$  cm) was calculated using the software PULSO (Neiff & Neiff, 2003). The water level values were obtained as the means of values from 6 days preceding sampling. According to Thomaz et al. (2004), the covariation between limnological variables and the water level is higher when considering the temporal average that precedes the sampling. Thus, Spearman's correlation was carried out to test the influence of water levels on the limnological variables, such as WT, EC, pH, and DO.

**Table 1** Mean values, standard deviation of the limnological variables and characterization of the hydrological cycles between March 2004 and January 2005 and between February

2007 and February 2013, in the Manezinho Backwater (Upper Paraná River Floodplain), during which ostracods were sampled for the present research

Hydrological cycles	Periods	WT (°C)	pH	EC ( $\mu\text{s cm}^{-1}$ )	DO ( $\text{mg l}^{-1}$ )	WL (cm)	Duration (No. days)	Months	No. samples
1	P1	28.8*	5.6*	51.8*	6.1*	415.0 $\pm$ 24.1	10	January 2005	3
	L1	24.4 $\pm$ 3.7	6.6 $\pm$ 0.6	61.0 $\pm$ 4.5	6.2 $\pm$ 2.5	250.3 $\pm$ 28.8	296	March to December 2004	30
2	P2	29.1 $\pm$ 0.6	7.0 $\pm$ 0.3	55.0 $\pm$ 3.0	5.2 $\pm$ 1.0	591.0 $\pm$ 0.1	38	February to March 2007	6
	L2	25.9 $\pm$ 3.8	6.6 $\pm$ 0.4	60.1 $\pm$ 6.2	4.9 $\pm$ 1.9	268.8 $\pm$ 22.6	275	April 2007 to March 2008	36
3	P3	24.5 $\pm$ 1.4	6.7 $\pm$ 0.4	57.8 $\pm$ 8.5	4.9 $\pm$ 2.5	388.1 $\pm$ 10.1	24	April to May 2008	6
	L3	24.8 $\pm$ 2.8	6.7 $\pm$ 0.7	55.8 $\pm$ 5.0	4.4 $\pm$ 2.3	259.8 $\pm$ 37.6	267	June 2008 to February 2009	27
4	P4	30.0 $\pm$ 2.7	6.6 $\pm$ 0.5	65.6 $\pm$ 3.8	6.2 $\pm$ 1.9	394.9 $\pm$ 7.8	19	March to April 2009	6
	L4	24.6 $\pm$ 2.7	6.3 $\pm$ 0.8	56.6 $\pm$ 6.5	4.5 $\pm$ 3.3	264.5 $\pm$ 25.6	176	May to November 2009	21
5	P5	28.6 $\pm$ 1.0	7.0 $\pm$ 0.3	68.9 $\pm$ 2.6	6.7 $\pm$ 1.7	514.7 $\pm$ 100.1	130	December 2009 to April 2010	15
	L5	23.5 $\pm$ 3.0	6.5 $\pm$ 0.4	56.9 $\pm$ 2.9	4.8 $\pm$ 1.9	285.1 $\pm$ 21.5	263	May 2010 to January 2011	27
6	P6	27.7 $\pm$ 2.0	6.9 $\pm$ 0.3	63.1 $\pm$ 7.9	6.3 $\pm$ 1.7	391.6 $\pm$ 37.8	65	February to May 2011	12
	L6	23.0 $\pm$ 3.5	6.9 $\pm$ 0.5	56.8 $\pm$ 11.4	6.0 $\pm$ 2.1	279.7 $\pm$ 19.7	226	June 2011 to January 2012	24
7	P7	28.5 $\pm$ 0.3	6.7 $\pm$ 0.1	62.7 $\pm$ 1.5	3.4 $\pm$ 0.8	428.7 $\pm$ 21.8	17	February 2012	3
	L7	25.9 $\pm$ 3.6	6.5 $\pm$ 0.4	52.2 $\pm$ 17.0	6.1 $\pm$ 2.2	283.5 $\pm$ 0.1	374	March 2012 to February 2013	36

*P* potamophase, *L* limnophase, *WT* water temperature, *EC* electrical conductivity, *DO* dissolved oxygen, *WL* water level of Paraná River

\* Only one measurement was done in the potamophase of cycle 1

The (dis)similarity (Bray–Curtis index) in ostracod species composition was analyzed between the hydrological periods. The first two axes of the principal coordinate analysis (PCoA) were retained, in accordance with the criteria of the Broken-Stick method,

and submitted to a one-way ANOVA. Both axes of the PCoA were used to test the influence of limnological factors on the ostracod community structure through Spearman's correlation.

The variability, or inversely the persistence, of the species composition of ostracod communities between subsequent periods and interperiods (see Fig. 1), was evaluated through the dispersion homogeneity test—PERMDISP (Anderson et al., 2006) using a density matrix. The test is based on the distances between the sample units for the centroid of the group, using a dissimilarity measure, within a dimensional space calculated by PCoA. The analysis was based on a dissimilarity matrix obtained using the Bray–Curtis index. Thus, higher mean Bray–Curtis distances suggest greater variability in ostracod species composition. The graphs were plotted according to each of the hydrological cycle (limnophase and potamophase). The level of significance between the limnophase and potamophase periods was analyzed using a permutation test for homogeneity of multivariate dispersions with 999 permutations. Significant differences were distinguished through a Tukey test. Spearman's correlation was used to evaluate the relationship between the PERMDISP values of each hydrological period with increasing time.

We have also checked for possible correlations between variability and duration of each period and between variability and number of samples within each period using Spearman's and Pearson's correlations.

Potential differences in variability between the three stations within the backwater were assessed with PERMDISP analyses, first with data per station for all seven cycles combined, and second with data per station for each cycle individually.

The analysis of indicator value (IndVal, Dufrene & Legendre, 1997) was carried out to test the potential of persistent ostracod species in limnophase (drought) and potamophase (flood) periods. A density data matrix of the ostracod species and the respective previously established category (hydrological periods) was used in each sampled month. This method consists in the identification of an index for each species  $i$  in each site group  $j$  ( $\text{IndVal}_{ij}$ ) calculated through the expression:  $\text{IndVal}_{ij} = A_{ij} \times B_{ij} \times 100$ ;  $A_{ij} = \text{Nindividuals}_{ij} / \text{Nindividuals}_j$ .  $B_{ij} = \text{Nperiods}_{ij} / \text{Nperiods}_j$ ,  $A_{ij}$  represents a measure of specificity and the elements of the formula are constituted by  $\text{Nindividuals}_{ij}$  [mean number of density of species  $i$  in the samples of group  $j$  (periods)],  $\text{Nindividuals}_j$  (sum of mean values of density of species  $i$  over all groups),  $A_{ij}$  is maximum when species  $i$  is found only in cluster  $j$ ,  $B_{ij}$  is the

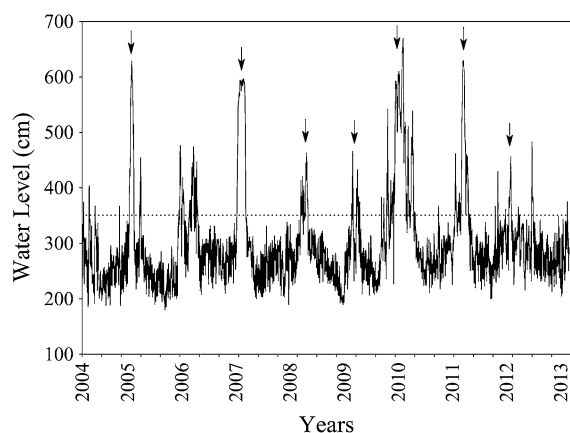
measure of fidelity and the elements of the formula are  $\text{Nperiod}_{ij}$  (number of samples from grouping  $j$  where species  $i$  is present),  $\text{Nperiod}_j$  (total number of samples in group  $j$ ),  $B_{ij}$  is maximum when species  $i$  is found in all samples of cluster  $j$ . The quantities  $A$  and  $B$  are combined by multiplication because they represent independent information on species distributions (results are expressed as percentage). The Monte Carlo test was used to test the significance of the IndVals of the species.

Analyses were performed using software R 3.3.1 (R Development Core Team, 2016) through the vegan (Oksanen et al., 2016), permute (Simpson, 2016) and lattice (Sarkar, 2008) packages. The species indicator test was processed in PC-Ord 6.0 software (McCune & Mefford, 1999). Analyses of variance and correlations were carried out with the program Statistica 7.1 (StatSoft, Inc., 2005).

## Results

### Abiotic variables

Figure 3 shows the variation of the water levels for all data series. During the monitoring, seven hydrological cycles were classified in limnophases (drought periods) and potamophases (flood periods, Table 1). The most intense drought period occurred in the first cycle



**Fig. 3** Daily average variation of the Paraná River water levels between March 2004 and February 2013. The dashed line represents the threshold between the hydrological periods (potamophase and limnophase), the arrows represent the potamophases (flood periods) considered for the present data analysis

(2004, 250.3 cm  $\pm$  28.8), the highest variation of the drought period was in the cycle 3 (2008–2009, 259.8 cm  $\pm$  37.6) and duration in the cycle 7 (2012–2013 for 374 days). The higher average value for the flood period was in the cycle 2 (2007, 591.0 cm  $\pm$  0.1) and the highest variation and duration of the high-water level was in the fifth cycle (2009–2010, 514.7 cm  $\pm$  100.1 for 130 days).

The results of Spearman's correlation between water level and limnological variables showed a positive and significant relation to WT ( $r = 0.39$ ,  $P = 0.000$ ), EC ( $r = 0.33$ ,  $P = 0.000$ ) and pH ( $r = 0.20$ ,  $P = 0.001$ ), evidencing an increment of these variables values when the water level was increased. DO also showed a positive trend with the increase of the water level, however, the correlation was not significant ( $r = 0.08$ ,  $P = 0.205$ , see also plots in Fig. S1). The mean values and standard deviation of the limnological variables for the seven hydrological cycles are shown in Table 1, during the period from March 2004 to February 2005 and from February 2007 to February 2013.

#### Composition and variability of the ostracod communities

The first two retained axes of PCoA showed significant differences in the species composition between hydrological periods (Axis 1:  $F = 2.011$ ,  $P = 0.000$  and Axis 2:  $F = 2.697$ ,  $P = 0.001$ ). Spearman's correlation between scores of axes of the PCoA and abiotic variables showed negative relations with WT (Axis 1:  $r = -0.27$ ,  $P = 0.000$ , Axis 2:  $r = -0.24$ ,  $P = 0.000$ ), EC (Axis 1:  $r = -0.21$ ,  $P = 0.000$ ) and water level (Axis 2:  $r = -0.13$ ,  $P = 0.004$ ), indicating higher similarity of the species composition with increase of the values these variables mainly in the potamophases (Fig. 4A, B, D, E). On the other hand, ostracods composition was positively correlated with pH (Axis 1:  $r = 0.14$ ,  $P = 0.024$ , Fig. 4C).

The dispersion homogeneity test (PERMDISP), used to investigate the variability, or inversely, persistence of the species composition of communities, showed significant differences between potamophase and limnophase periods ( $F = 8.47$ ,  $P = 0.00$ ). The variability in species composition during the potamophases was always much smaller than in the limnophase, except in the potamophase

period of cycle 5 (2009–2010) and to a lesser degree in cycle 6 (2011–2012, Fig. 5).

No correlation was observed between community variability and duration of each period and between community variability and number of samples within each period. Results of Spearman's correlation for limnophase periods: variability and number of samples ( $P = 0.64$ ), variability and duration of periods ( $P = 0.70$ ). Results of Pearson's correlation for potamophase periods: variability and number of samples ( $P = 0.62$ ), variability and duration of periods ( $P = 0.62$ ).

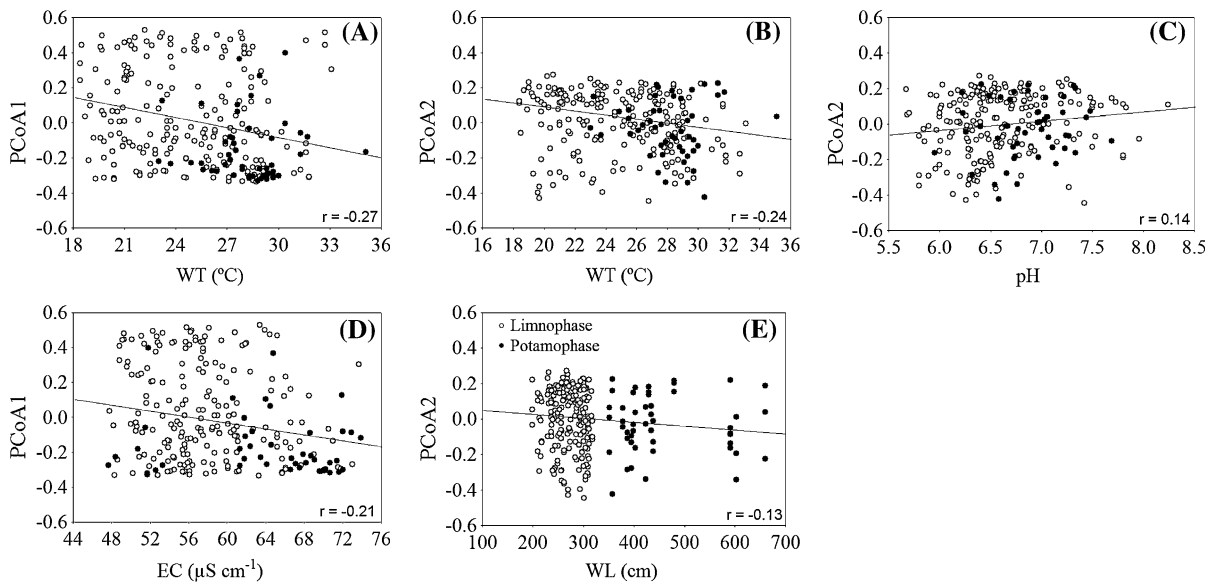
The community variability, measured as the average distance of the sample units for the centroid, was highest in the limnophase periods of cycle 5 (2010–2011, 0.47) and cycle 7 (2012–2013, 0.46), and the potamophase of cycle 5 (2009–2010, 0.43), while the lowest mean distance was in the potamophase period of the first cycle (2005, 0.11), followed by the potamophase of cycle 4 (2009, 0.20) and the potamophase of cycle 2 (2004, 0.22, Fig. 5). Figure 6 shows that the values of the dispersion measure increased significantly over time, as evidenced by the Spearman's correlation ( $r = 0.62$ ,  $P = 0.017$ ).

The results of the Tukey test showed, during the subsequent periods, that ostracod communities were persistent since the potamophase of cycle 1 (2004) to the limnophase of cycle 4 (2009); and the limnophase of cycle 5 (2010–2011) to the limnophase of cycle 7 (2012–2013). The community was variable only in the potamophase of cycle 5 (2009–2010), which comprised an extreme flood with long duration. Considering interperiods, we observed variability of composition after the extreme flood (cycle 5, Table 2).

The PERMDISP analyses of the variability of species composition in the three stations for all cycles combined showed that there were no significant differences between the three stations ( $F = 0.4407$ ,  $P = 0.6441$ , Fig. S2). Similar analyses for the seven cycles separately showed similar absence of significant differences, except for cycle 4 (Fig. S3).

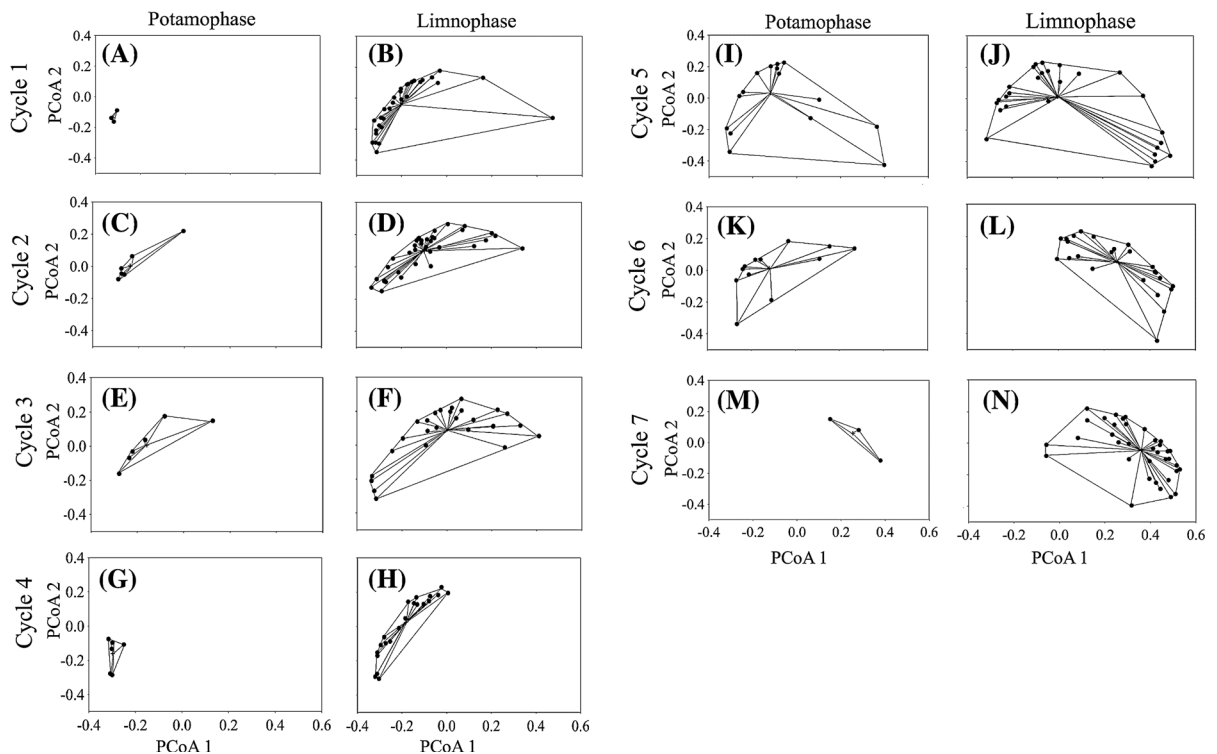
#### Indicator species

In total, 34 ostracod species were recorded belonging to four families. Cyprididae was the most numerous family, with 22 species, followed by Candonidae, Darwinulidae, and Limnocytheridae. *Diaphanocypris*



**Fig. 4** Significant Spearman's correlations between scores of Axes 1 and 2 of the PCoA and abiotic variables from March 2004 to January 2005 and from February 2007 to February 2013.

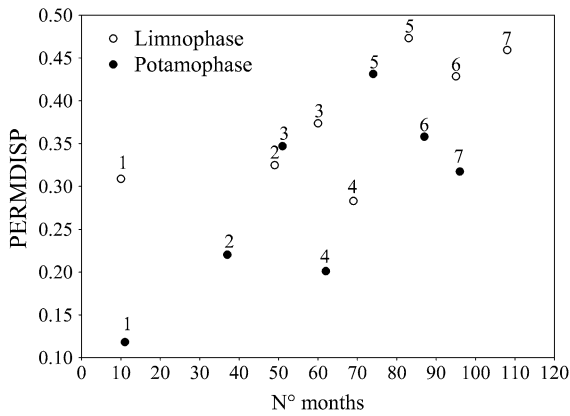
*WT* water temperature (A, B), *pH* (C), *EC* electrical conductivity (D) and *WL* water level (E)



**Fig. 5** Multivariate permutation PCoA diagram showing the variation in the ostracod species composition in both phases (potamophase and limnophase) of the seven hydrological

cycles. The lines indicate the maximum dispersion of sample units for each hydrological period. The center from where the lines radiate represents the respective centroid group





**Fig. 6** Mean distance of the sample units to the centroid evaluated through the dispersion homogeneity test (PERMDISP) in each hydrological cycle. The X-axis shows the number of months of the start of each hydrological cycle in relation to the end of the first limnophase period (2004). The numbers (1–7) represent the hydrological cycles, their durations are described in Table 1

*meridana* (Furtos, 1936), *Strandesia lansactohai* Higuti & Martens, 2013, *Bradleystrandesia trispinosa* (Pinto & Purper, 1965), *Cypricercus centrura* (Klie,

1940), *Cyprretta costata* (G. W. Müller, 1898), *Cabellodopsis hispida* (Sars, 1901), *Cytheridella ilosvayi* (Daday, 1905), *Alicenula serricaudata* (Klie, 1935), *Vestalenula pagliolii* (Pinto & Kotzian, 1961), and *Penthesilenula brasiliensis* (Pinto & Kotzian, 1961) were recorded in all hydrological periods. *Strandesia variegata* (Sars, 1901) occurred exclusively in the limnophase period of the fifth cycle (2010–2011), *Strandesia* sp. 7 n.sp. only in the limnophase period of the fourth cycle (2009) and *Physocypria* sp. 2 n.sp. in the limnophase period of the sixth cycle (2011–2012, Table S1).

Results of the species indicator test (IndVal) showed that *D. meridana*, *Strandesia mutica*, *C. centrura*, *Chlamydotheca iheringi*, *Cypridopsis* cf. *vidua* sp. 2, “*Cypridopsis*” sp. 1 n.gen. n.sp., “*Cypridopsis*” sp. 2 n.gen. n.sp., *C. hispida*, *C. ilosvayi*, *A. serricaudata*, *V. pagliolii*, and *P. brasiliensis* were indicative of potamophase periods, which means that these species were persistent in the flood periods (Table 3). No indicator species were found for the limnophase periods.

**Table 2** Variability and persistence of the ostracod community between subsequent periods and between interperiods in the Manezinho Backwater (Upper Paraná River Floodplain)

Hydrological cycles		Variability (Var) and Persistence (Per)													
		1		2		3		4		5		6		7	
		P1	L1	P2	L2	P3	L3	P4	L4	P5	L5	P6	L6	P7	L7
Tukey test (PERMDISP)	1	P1	Per	Per	Per	Per	Per	Per	Per	Var	Var	Per	Var	Per	Var
		L1		Per	Per	Per	Per	Per	Per	Per	Var	Per	Var	Per	Var
	2	P2		Per	Per	Per	Per	Per	Per	Var	Var	Per	Var	Per	Var
		L2			Per	Per	Per	Per	Per	Per	Var	Per	Per	Per	Var
	3	P3			Per	Per	Per	Per	Per	Per	Per	Per	Per	Per	Per
		L3				Per	Per	Per	Per	Per	Per	Per	Per	Per	Per
	4	P4				Per	Per	Per	Per	Per	Per	Per	Per	Per	Per
		L4					Per	Per	Per	Per	Per	Per	Per	Per	Per
	5	P5	0.008		0.040			0.014	0.038		Per	Per	Per	Per	Per
		L5	0.000	0.000	0.001	0.000		0.000	0.000		Per	Per	Per	Per	Per
	6	P6								Var	Var	Per	Var	Per	Per
		L6	0.006	0.039	0.024			0.007	0.010			Per	Per	Per	Per
	7	P7												Per	Per
		L7	0.001	0.000	0.002	0.001		0.000	0.000						Per

The P values of the Tukey test are arranged below of the diagonal line  
 P potamophase, L limnophase

## Discussion

### Abiotic variables

In the Upper Paraná River Floodplain, the water level during the limnophase period may change from few days to several months throughout the year, as for example in 2004 and 2012–2013 (cycles 1 and 7, respectively). The same was true for the potamophase period in 2009–2010 (cycle 5). The occurrence of several oscillations of the flood pulses is mostly associated with the operation of man-made dams that regulate and alter the natural hydrological regime of the Paraná River (Thomaz et al., 2004; Souza Filho, 2009). Also, the natural variations in precipitation caused by El Niño play a role. In this way, the dynamics of the abiotic variables (local scale) are closely linked to the variations of the flood pulses (regional scale), as evidenced by the Spearman's correlations (see above), and consequently alter the composition of ostracod communities (see below).

Extreme floods in South America, especially in southern Brazil, are associated with the El Niño phenomenon, which leads to irregular flood pulses in river–floodplain systems (Grimm & Tedeschi, 2009; Ward et al., 2010, 2014; Räsänen & Kumm, 2013). In the 2009–2010 (cycle 5), for example, the higher waters level in the Paraná River were directly linked to the occurrence of an El Niño event. This was only one of a series of marked El Niño events since the beginning of the twenty first century (Yu & Kim, 2013) which caused extreme climatic anomalies around the world (Lee et al., 2010; Seager et al.,

2010; Kim et al., 2011; Ratnam et al., 2012). In addition, several dams upstream of the Upper Paraná River Floodplain released higher volumes of water and, together with the El Niño event, this caused the extreme flood (CPTEC, 2016) during the potamophase of hydrological cycle 5 (2009–2010).

### Composition and variability of ostracod communities

Changes in species composition were observed between potamophase and limnophase periods, because of the homogenization effects of the higher water levels on ostracod communities during the potamophases. These homogenizing effects lead to increase of the similarity of species composition of the ostracod communities. Organisms can develop morphological, physiological, and phenological adaptations to natural flood pulses, with recurrent intervals and frequencies, thus reducing potential negative effects of such regular flood pulses (Junk & Wantzen, 2007). Such adaptations will also buffer effects of flood pulses when they are regulated by man-made dams (Robinson & Uehlinger, 2006). In addition, “normal” flooding increases habitat similarity by minimizing resource variation (Thomaz et al., 2007) and, in response, causing decreasing community structure variability under relatively homogenous and constant environmental conditions (Bengtsson et al., 1997). Flood pulses usually occur during summer and the accompanying higher temperatures might accelerate the life cycle of ostracods (Smith et al., 2015). In the potamophase periods during the

**Table 3** Indicator ostracod species of the potamophase period in the Manezinho Backwater (Upper Paraná River Floodplain)

	Species	Abundance (%)	Frequency (%)	IndVal	Value of <i>P</i>
	<i>Diaphanocypris meridana</i>	70	94	65	0.001
	<i>Strandesia mutica</i>	92	10	9	0.008
	<i>Cypricerus centrura</i>	61	100	61	0.003
	<i>Chlamydotheca iheringi</i>	92	14	13	0.043
	<i>Cypridopsis</i> cf. <i>vidua</i> sp. 2	76	10	7	0.040
	“ <i>Cypridopsis</i> ” n. gen. 1 n.sp.	87	24	20	0.001
	“ <i>Cypridopsis</i> ” n. gen. 2 n.sp.	70	73	51	0.001
	<i>Cabelodopsis hispida</i>	69	98	68	0.001
	<i>Cytheridella ilosvayi</i>	61	98	60	0.025
	<i>Alicenula serricaudata</i>	66	88	59	0.005
There were no indicator species for the limnophase periods	<i>Vestalenula pagliolii</i>	59	96	56	0.041
	<i>Penthesilenula brasiliensis</i>	60	88	53	0.043

present study, the wider range of the limnological variables (e.g., temperature, conductivity and pH) contributed to the increase of similarity in species composition (see Fig. 4) and consequently to the decrease of the species composition variability (see Fig. 5). However, an increase of the ostracod species composition variability was observed in the extreme flood with longer duration (the potamophase of cycle 5). This is unexpected as such extreme floods will further augment the exchange of organisms through the aquatic connections between lakes and rivers. It is possible that extreme floods may trigger the hatching of dry-resistant eggs (see discussion of “Indicator species” section). In this way, the persistence of the community structure between successive periods from the potamophase of cycle 1 to the limnophase of cycle 4 may be associated with lower intensity of the disturbances, which do not significantly interfere with the ostracod community structure.

We have found that ostracod species composition variability within periods in both limnophases and potamophases are not correlated to neither the duration of, nor to the number of samples within these periods, which means that comparisons between these units are valid.

Some periods of the hydrological cycles were discrete, with a short duration or little variation, as in the floods of 2009 and 2012 (cycles 4 and 7, respectively). Higiuti et al. (2007) argued that free-floating macrophytes accompany the water level and this does not become a limiting factor in the density change of the ostracod communities. Indeed, during such discrete events, ostracod abundances did not change significantly in the Manezinho Backwater, indicating buffering and high persistence of community structure. Other studies have demonstrated similar persistence of community structure in several aquatic groups, such as macroinvertebrates (Scarsbrook, 2002; Collier, 2008), phytoplankton (Schneck et al., 2011), and cichlid fish (Lourenço et al., 2012), indicating resistance to natural disturbances of short durations (see also “Introduction” section). In contrast, planktonic crustacean communities in a Polish oxbow lake experienced a marked decrease in densities with increasing water levels during the potamophases (Napiórkowski & Napiórkowska, 2017).

Other differences in the variability in the ostracod species composition between interperiods, such as the potamophase of cycle 1 (2005) and the limnophase of

cycle 5 (2010–2011, Table 2), were also owing to longer duration of the flood, in this case caused by a sequence of successive floods and especially by the extreme flood (potamophase of cycle 5). Studies of other aquatic communities have demonstrated the increase in the variability of community structure over time owing to greater fluctuation of environment conditions, as fish (Oberdorff et al., 2001) and macroinvertebrates (Brown et al., 2006; Bêche & Resh, 2007).

#### Ecological disturbance

Since 2008, the Manezinho Backwater was increasingly colonized by a native submerged macrophyte (e.g., *Egeria najas* Planch.) while the stands of *E. crassipes* dwindled by the middle of 2013, and few individuals of *E. crassipes* remained in this backwater. This is why the present monitoring program had to be stopped in that year. Propagules of *E. najas* established in the backwater in 2008, and possibly interfered in the variability of species composition during its colonization, as shown by the reduced variability in cycle 4 (see Fig. 6). Studies developed in lentic environments, e.g., reservoirs, showed that *E. najas* occur between 2 and 4 m deep, with a growth coefficient between 0.022 and 0.082 day<sup>-1</sup> and a doubling time between 8.5 and 31.5 days, with aquatic radiation and turbidity being the main limiting factors for its expansion (Thomaz et al., 2003). This species can achieve a large standing biomass and competition between macrophytes and/or habitat preference of some ostracods (Mormul et al., 2010) may have also contributed to the decrease in the variability of species composition in cycle 4. An increase of composition variability was observed between 2008–2009 (cycle 4) and 2009–2010 (cycle 5, see Fig. 6), indicating the effects of the extreme flood pulses and minimizing the effects of *E. najas* on the ostracod communities. Thereafter, the variability of the ostracod species composition remains relatively high, when compared to cycle 5. The roots of free-floating macrophytes, mainly of *E. crassipes*, offer a substrate of high complexity that allows the occurrence of several species in high abundances (Higiuti et al., 2007; Matsuda et al., 2015), allowing immigrant individuals to cohabit with the others.

In addition to the invasion of *E. najas*, the connecting channel between the lake and the river

started silting up since c 2011, so that even during the regular floods of cycles 6 and 7, less connectivity occurred during these potamophases.

### Indicator species

The potamophase periods allow the addition of new individuals by immigration through the water connections formed by the flood, as proposed by Thomaz et al. (2007), as well as the creation of new opportunities for temporal niches (Chesson & Huntly, 1997). Some species were more abundant during the potamophase periods, as evidenced by the test of indicator species, most of which belong to the family Cyprididae (see Tables S1, 3). Ostracod species of this family can produce dry-resistant eggs (Meisch, 2000) that can hatch irregularly over different generations (Smith et al., 2015). The floods might thus have contributed to the hatching of eggs that were not inundated in the limnophase, for example because they were attached to dried macrophytes, remnants of the previous potamophase, hanging several meters high in the trees.

*Alicenula serricaudata*, *V. pagliolii*, and *P. brasiliensis* (family Darwinulidae) do not produce dry-resistance eggs, but may benefit from the increased potential for colonization during potamophase periods. In addition, high temperatures (which coincide with the flooding period in summer) might increase the metabolic rate of organisms, resulting in shorter life cycles, as proposed for Darwinulidae by Higuti et al. (2009). However, this remains to be tested in controlled experiments.

### Conclusions

Our hypothesis that during regular flood pulses the ostracod communities were stable and persistent, while in the extreme and long duration floods there was markedly more variability, is here corroborated. It should be stressed that the difference between regular and extreme floods could only be detected in the course of a long term, multi-annual monitoring program. Most ecological studies span one to a few years only, because funding for research projects is mostly for 2–4 years. The present results show the importance of long term ecological monitoring programs for the detection of the effects of extreme and rare events.

Our results are relevant for understanding the dynamics of the ostracod community structure, and as a model for pleuston communities in general. Such understanding is important for decision-making by natural resources managers, because large-scale environmental changes are expected as a result of global climate change and, consequently, significant changes in community structure might be expected. For rivers with many man-made dams, such as the Upper Paraná River, the effects of extreme floods resulting from unpredictably increased precipitation could at least partly be moderated by regulating water release from these dams. This would require that the authorities in charge of these dams take ecosystem health of downstream floodplains into account when deciding on their water release schedules.

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