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ORIGINAL ARTICLE



A comparison between active and passive communities of Ostracoda (Crustacea) in a tropical temporary lake

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ABSTRACT

Some microcrustaceans living in temporary waterbodies produce drought-resistant stages under adverse conditions. These structures accumulate in the sediment, forming an egg bank in which eggs can remain viable for many years. Here, we evaluate the contribution of ostracod resting eggs to the structure of the active ostracod community in a tropical temporary lake located in the Upper Paraná River floodplain, Brazil. The active ostracod communities were sampled by hand net, while sediment samples (egg banks) were collected using a core sampler. Sediments were oven-dried, then re-hydrated with filtered lake water and kept in hatching chambers. A total of 13 ostracod species were recorded, eight species in the passive community, and nine species in the active community, four species were recorded in both communities. The species composition between active and passive communities was significantly different. Five species of the active community could be of allochthonous origin and are most likely introduced by flooding or by other dispersal vectors. In conclusion, the egg bank adds species not necessarily found in the active community, thus acting in the maintenance and enrichment of the local and regional faunas.

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Microcrustaceans; dormancy; potential invasive; extreme weather events; floodplain

Introduction

Temporary waters are habitats with recurrent cycles of wet and dry periods. Temporary pool or lake animals either survive the dry periods in the same locality as drought-resistant stages, such as crustaceans and rotifers, or they recolonize the freshly inundated habitat from elsewhere, such as amphibians and flying insects (Williams 2006; Sim et al. 2013; Radzikowski 2013). The first group of aquatic communities thus has two distinct life phases: the active phase, with living animals being present in wet conditions, and the passive or dormant phase, characterized by the presence of drought-resistant or dormant stages in the sediments (Radzikowski 2013; Walsh 2013). The egg banks can promote the coexistence of species and contribute to the resilience of aquatic communities (Pimm 1984; Brendonck & De Meester 2003; Santangelo et al. 2011).

Microcrustaceans are amongst the most common organisms found in temporary environments (Williams 1997; Hay et al. 2018), and many freshwater ostracods (Crustacea) can produce resting eggs, especially species of the family Cyprididae (Horne & Martens 1998). Ostracod resting eggs accumulate in the sediment over several

generations and seasons, forming the egg banks, and can remain viable for many years (Angell & Hancock 1989; Martens 1994). Not all families of freshwater ostracods produce drought-resistant eggs (e.g. Darwinulidae do not), and other structures and strategies can be used by ostracods to avoid desiccation, such as torpidity in certain Candonidae (Delorme & Donald 1969).

The recruitment of the active community by hatching of resting eggs occurs when conditions of the environment become favorable, e.g. presence of sufficient water with suitable biotic and abiotic conditions (Radzikowski 2013; Hay et al. 2018). However, some eggs may remain in dormancy, even though environmental conditions are appropriate to survive. This strategy, in which some eggs hatch quickly, while others stay dormant for long periods, fits in to the concept of 'bet-hedging'. Philippi and Seger (1989) described bet-hedging as an evolutionary trade-off between the mean and variance of fitness, where an individual sacrifices expected fitness to reduce temporal variance in reproductive success. This strategy serves as a protection against potential future catastrophic events in a habitat, such as drying of the habitat before the organisms could complete their life

cycle and produce new resting eggs (Evans & Dennehy 2005).

Hatching of resting eggs can be triggered by environmental, abiotic, and biotic stimuli (Gyllström & Hansson 2004). For instance, water level and hence hydrostatic pressure have been shown to be an important factor for the hatching of resting eggs (Brendonck 1996; Williams 2006). In addition, temperature, day-light length, and other physical factors can also stimulate hatching (Paes et al. 2016). Timing and success of hatching can also be influenced by epigenetic factors, such as maternal effects since the phenology of the eggs can also be related to factors already experienced by the mother organisms. For example, the environment in which the mother lived can act as triggers for the hatching of resting eggs under specific circumstances (De Meester & De Jager 1993). On the other hand, the presence of large predators such as fish and amphibians or even their kairomones alone can inhibit hatching (Blaustein 1997). In addition, the viability of resting eggs will reduce over time, owing to exposure to ultraviolet radiation, burial, and other factors (Brendonck 1996; Gleason et al. 2003).

Resting eggs play an important role in the structuring of populations and communities since they are an alternative source of organisms for the active community. In addition, they can increase the dispersal potential of organisms, since they can be dispersed by both biotic and abiotic vectors over long distances. Resting eggs can thus increase the genetic and taxonomic biodiversity of both the passive and the active communities (Ellner & Hairston 1994; Brendonck et al. 2017).

Studies on passive communities are important to understand the functioning and dynamics of active communities over time because egg banks often harbor greater richness of species compared to the active community (Crispim & Watanabe 2001). Several studies have demonstrated that zooplankton egg banks contribute to the taxonomic richness of the active community (Hairston 1996; Crispim & Watanabe 2001). For example, Palazzo et al. (2008a) recorded a cladoceran species for the first time in the Paraná River floodplain by hatching it from the egg bank from a temporary lake. However, few studies have addressed the evolutionary ecology of resting eggs of ostracods.

Here, we evaluate the contribution of ostracod resting eggs from the passive community to the structure of the active community in a tropical temporary lake. We test the following hypotheses: (1) species composition of the passive community (the egg bank) differs from the active community owing to the potential accumulation of eggs over several generations and

seasons; (2) species of the active community can also be of allochthonous origin.

Material and methods

Study area

Osmar Lake is located in the Upper Paraná River floodplain, which belongs to the Environmental Protection Area of the 'Várzea' Islands of the Paraná River, Brazil. This floodplain is composed of a wide variety of environments, including rivers, channels, isolated and permanently connected lakes, backwaters, temporary lakes, and ponds (Thomaz et al. 2004). The pluvial regime is characterized by a rainy (November to March) and a dry season (April to October) (Agostinho et al. 2004). Osmar Lake (22°46'27.53"S and 53°19'57.95"W) is an isolated and elongated lake (about 60 m long and 15 m wide, with a mean depth of 1.1 m), located on Mutum Island, on the right bank of the Paraná River (Roberto et al. 2009; Mormul et al. 2012) (Figure 1). This lake, classified as 'temporary' following Williams (2006), has recurrent sequences of droughts and inundations (Bertoncin et al. 2019). The riparian vegetation of lake Osmar shelters remnants of both forest and aquatic macrophytes, such as *Oxycaryum cubense* (Poepp. and Kunth) Palla, *Polygonum punctatum* Elliot and *Polygonum ferrugineum* Wedd (Thomaz et al. 2009; Ferreira et al. 2016). During March and November 2004, March and September 2017, March and September 2018 the water temperature ranged between 20.5°C and 28.3°C. The pH of the lake was slightly acidic, ranging from 5.5 to 7.1. The range of variation of electrical conductivity was from 44.6 to 96.4 $\mu\text{S}\cdot\text{cm}^{-1}$ and low values of dissolved oxygen were observed in the lake, ranging from 0.6 to 4.8 $\text{mg}\cdot\text{L}^{-1}$.

The water level dynamics of the Paraná River over time show several major floods in the floodplain between 2004 and 2018 (Figure 2A). According to Souza Filho (2009), the water level of 350 cm is considered to be a reference value for overflow in the Upper Paraná River floodplain. A prolonged drought period with the lowest water levels occurred in 2015, during the collection of the passive community (Figure 2A). A large amplitude of precipitation occurred during 2004 and 2018 (Figure 2B). However, at the actual times of collecting the passive and active communities (2004, 2015, 2017, and 2018), there was less precipitation (Figure 2B).

The passive community

Considering that drying pools will accumulate biota at the deepest, mostly central, part of the lake where

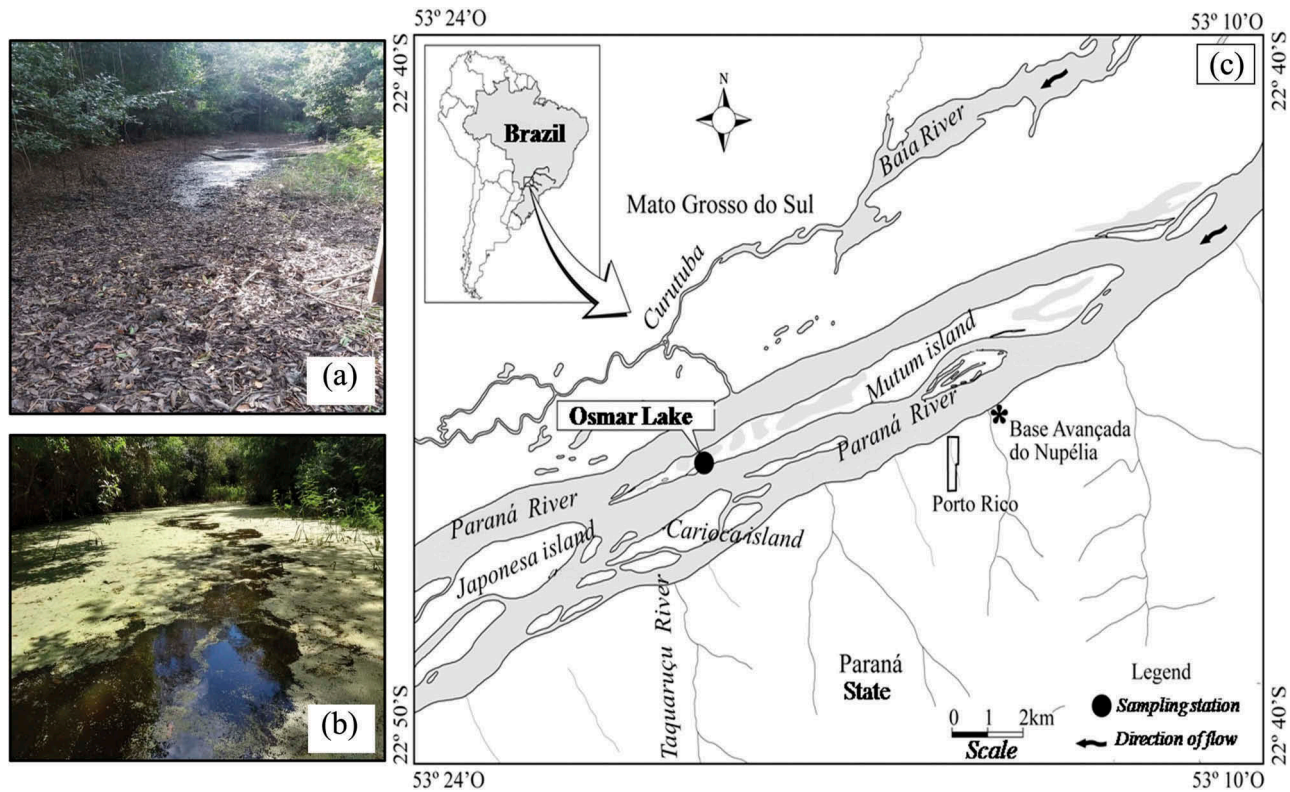


Figure 1. (a) Osmar Lake during the drought period (July 2018); (b) Osmar Lake during the flooding period (November 2018); (c) Location of Osmar Lake in the Upper Paraná River floodplain, Brazil.

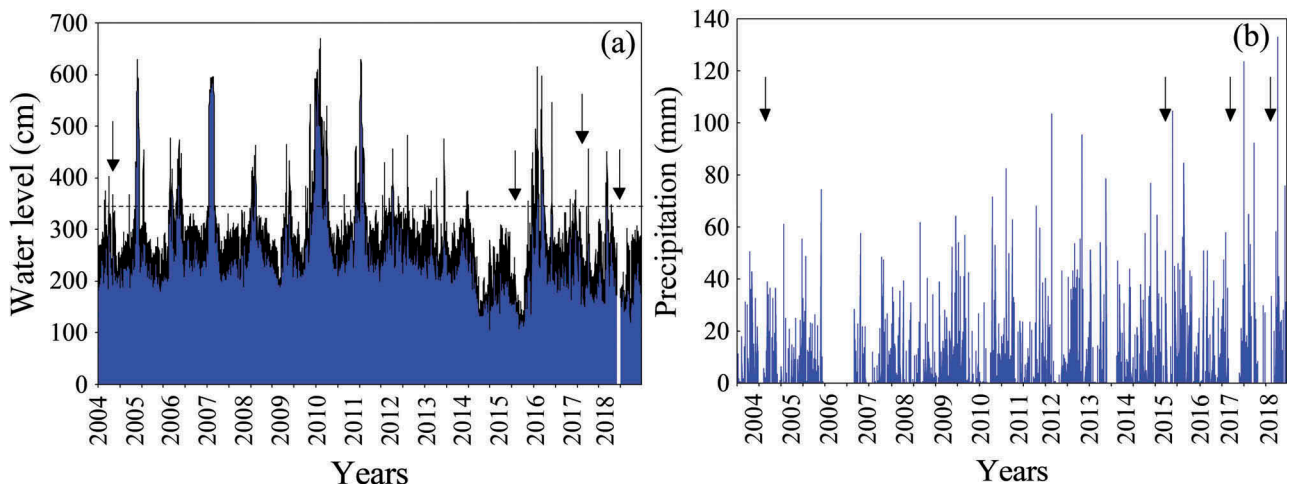


Figure 2. Water level variation of Paraná River (a) from 2004 to 2018; and precipitation values (b) from 2004 to 2018 at the meteorological station Porto Rico, Brazil. The arrows indicate the times of sampling.

resting eggs will be produced and laid by adults (Rosa et al. 2020), the sediment was sampled in two random sites of the central region of the Osmar Lake, using a core sampler. The sediment, to a depth c. 5 cm, was collected monthly during the dry period (May to September 2015). The sediment samples, approximately 500 grams, were stored in plastic bottles and kept under refrigeration at 4°C according to the

protocol of Maia-Barbosa et al. (2003), until the hatching in March 2017.

Artificial microcosms in plastic trays of 1 L were prepared for hatching the ostracod resting eggs, from five drought months and two sites of the lake, totaling 10 samples. The following protocol was used for hatching of resting eggs. First, the complete samples, i.e. 500 g of each of 5 months from two sites of the lake were

placed in an oven at 50°C for 24 hours to completely dry the sediment. Then, the samples were hydrated with 500 ml lake water, which was previously filtered through a phytoplankton net of 10 µm mesh size, and kept in the germination chamber at 25°C, with photoperiod 12 hours/light and 12 hours/dark for 149 days.

The incubation period was monitored in three phases: during the first period of 14 days, microcosms were checked every 2 days, during the second period of 105 days they were checked weekly, and during the third period of the next 30 days they were checked every 15 days. At each monitoring time, all the water from the microcosm was filtered with a plankton net of 15 µm mesh size, after which the trays were refilled with filtered lake water using a phytoplankton net of 10 µm mesh size. Living individuals were immediately sorted from the samples and all ostracod specimens were separated from other organisms and detritus under a stereomicroscope. Juvenile ostracods were stored separately alive in petri dishes and were kept in a germination chamber, in the same conditions as the hatching resting eggs experiment, until they reached the adult stage, unless the juveniles died earlier, for species identification.

The active community

Living ostracods from Osmar Lake were collected in March and November 2004, in March and September 2017, and in March and September 2018, thus yielding six samples in total. Sampling was done by hauling a rectangular net, 28 × 14 cm, mesh size 160 µm, close to the water–sediment interface in the littoral region of the lake and amongst macrophytes. The samples were preserved in ethanol 70% and subsequently sorted under a stereomicroscope Olympus SZ2-ILST. Ostracods were identified at species level using published keys and articles (e.g. Martens & Behen 1994 and references therein; Higuti & Martens 2012, 2014; Higuti et al. 2013).

Data analysis

The Welch t-test was performed to test significant differences in richness and abundance between the passive and active ostracod communities. Since the assumptions of normality and homoscedasticity were not fulfilled, parametric tests were not possible. Rarefaction curves compare species richness between passive and active communities at comparable levels of numbers of individuals (Gotelli & Colwell 2001).

A Principal Coordinate Analysis (PCoA) was used to visualise (dis)similarity of species composition for the passive and active communities, based on a matrix with the ten

samples of the passive and the six samples of the active communities, using the Jaccard distance (Legendre & Legendre 1998). During the analyses, the samples with zero individuals were automatically excluded. A Multivariate Permutational Variance Analysis, PERMANOVA, function ‘Adonis’ (Anderson 2001) was performed to evaluate differences in ostracod species composition between passive and active communities. The test was based on a dissimilarity matrix using the Jaccard distance with the same dataset used in the PCoA. A total of 999 permutations were performed to assess the significance of differences.

The dispersion homogeneity test, PERMDISP, function ‘betadisper’ (Anderson 2006) was performed to test the variability in the ostracod species composition, the beta diversity, between passive and active communities. This analysis is based on the distances between the sample units and the centroid of the group, using the same dataset used in the PCoA and the dissimilarity measure (Jaccard), within a dimensional space calculated by PCoA. A higher mean of the Jaccard distance corresponds to a higher variability in species composition. The significance level ($p < 0.05$) of the variability in ostracod species composition between active and passive communities was tested using a permutation test with an Analysis of variance (ANOVA). Statistical analyses were carried out with software R 3.2.4 (R development core team 2018), using the vegan (Oksanen et al. 2016) and permute (Simpson 2018) packages. Rarefaction analysis was performed using BioDiversity Pro version 2 software (McAleece et al. 1997).

Results

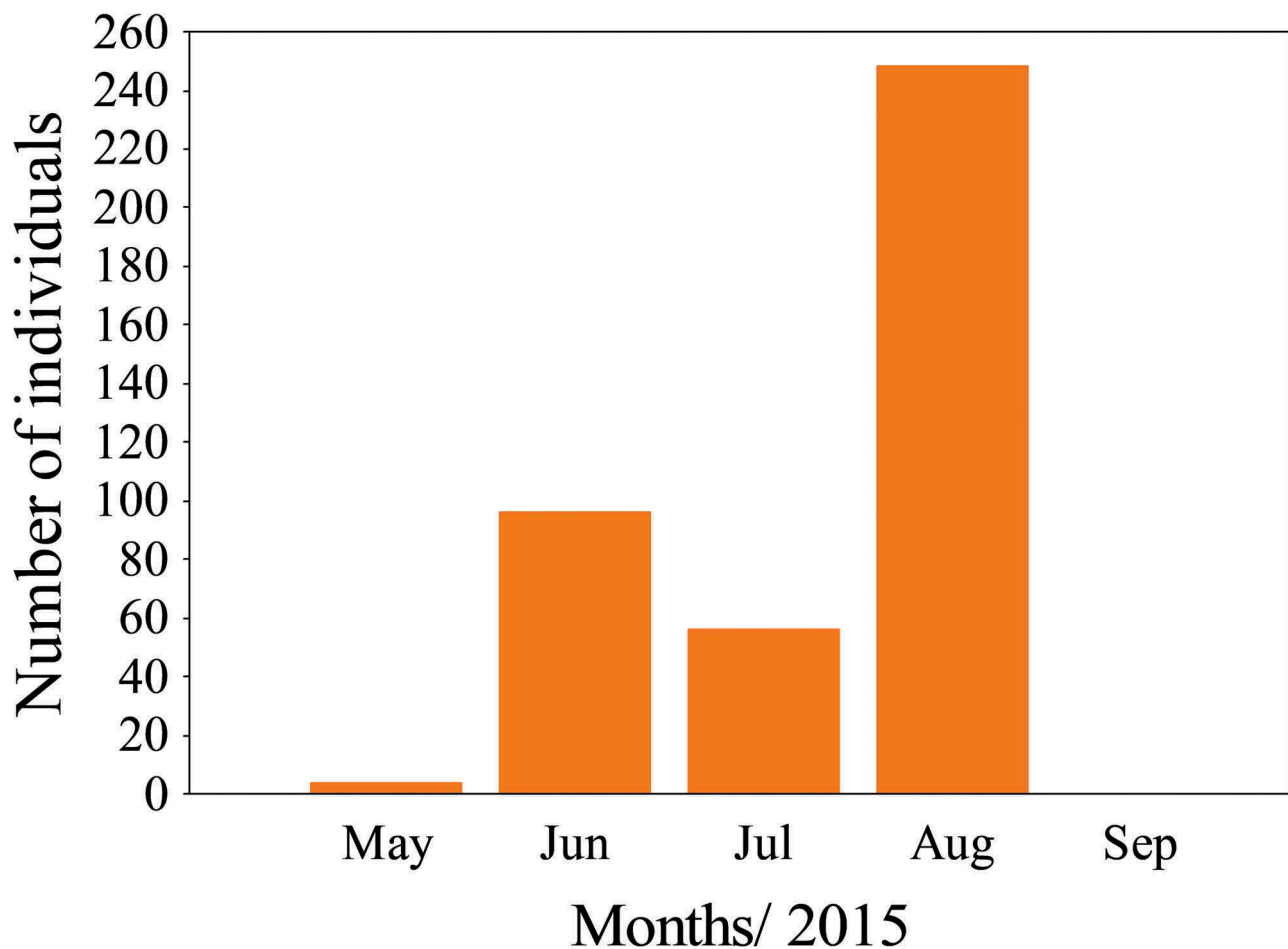
The passive community

A total of 405 individuals representing 8 ostracod species hatched from the egg banks over the 149 days of incubation. All hatched species belong to the family Cyprididae (Table 1). The highest numbers of specimens and species were recorded in August 2015 (248 individuals and five species). No ostracods hatched from the sediment that was collected in September 2015 (Figure 3).

Strandesia bicuspis (Claus, 1982) was the most abundant and frequent hatched species, representing 34% of the total number of hatched individuals. The second most abundant ostracod species was *Strandesia nupelia* Higuti and Martens, 2013 in June, July, and August 2015, represented by 23% of the total number of individuals. *Chlamydotheca iheringi* (Sars, 1901) was abundant in August 2015 comprising 19% of the total number of individuals. *Diaphanocypris meridana* (Furtos, 1936)

Table 1. Composition, richness, and number of individuals of ostracod species in the active community in 2004, 2017, and 2018, and in the passive community in 2015 of Osmar Lake in the Upper Paraná River floodplain.

	ACTIVE COMMUNITY						PASSIVE COMMUNITY				
	2004		2017		2018		2015				
	Mar	Nov	Mar	Sep	Mar	Sep	May	Jun	Jul	Aug	Sep
Family Cyprididae (Baird, 1845)											
<i>Chlamydotheca colombiensis</i> (Roessler, 1985)						20					
<i>Chlamydotheca iheringi</i> (Sars, 1901)						1		1		75	
<i>Cypricercus</i> sp. nov.								3	1		
<i>Cypridopsis</i> cf. <i>vidua</i>	32	4						1	21		
<i>Diaphanocypris meridana</i> (Furtos, 1936)	20										25
<i>Strandesia bicuspsis</i> (Claus, 1982)						363	3	19	23	95	
<i>Strandesia lansactohai</i> Higuti and Martens, 2013								6			
<i>Strandesia nupelia</i> Higuti and Martens, 2013								54	12	27	
<i>Strandesia velhoi</i> Higuti and Martens, 2013							1	6		11	
Family Candonidae (Kaufmann, 1900)											
<i>Candobrasilopsis brasiliensis</i> (Sars, 1901)			1								
<i>Candobrasilopsis rochai</i> Higuti and Martens, 2012		4									
<i>Pseudocandona agostinhoi</i> Higuti and Martens, 2014	8										
Family Limnocytheridae (Klie, 1938)											
<i>Cytheridella ilosvayi</i> Daday, 1905	24	136	41		20	3					
Ostracoda juvenile	32							6		15	
Richness	4	3	2	-	1	4	2	7	4	5	-
Number of individuals	116	144	42	-	20	387	4	96	57	248	-

**Figure 3.** Number of individuals hatched from the passive community, from May to September 2015, in Osmar Lake in the Upper Paraná River floodplain.

was found exclusively in August and *Strandesia lansactohai* Higuti and Martens, 2013 exclusively in June 2015, representing 6% and 1.5%, respectively, of the total number of individuals (Table 1).

The active community

In the active community, we recorded nine species of ostracods, represented by five Cyprididae, three Candonidae, and one Limnocytheridae (Table 1). Higher taxonomic richness was observed in March 2004 (four species) and September 2018 (four species), and higher abundance of ostracods was found in September 2018 (Figure 4). Juvenile ostracods were only recorded in March 2004 and no ostracods at all were found in the sample of September 2017 (Figure 4).

The species Cyprididae, *Chlamydotheca colombiensis* (Roessler, 1985) was recorded only in the active community in September 2018. *Strandesia bicusps* was recorded only in September 2018 and it was the most abundant species in the active community, representing 54% of all

individuals collected at that time (Table 1). *Chlamydotheca iheringi* was found in September 2018, *Cypridopsis* cf. *vidua* in March and November 2004, and *Diaphanocypris meridana* was recorded only in March 2004.

Three species of Candonidae were recorded only in the active community, *Pseudocandona agostinhoi* Higuti and Martens, 2014 and *Candobrasilopsis rochai* Higuti and Martens, 2012 were observed in March and November 2004, respectively. *Candobrasilopsis brasiliensis* (Sars, 1901) was found in March 2017 (Table 1).

Cytheridella ilosvayi Daday, 1905 (Limnocytheridae) was recorded in all samples except in September 2017 and it was the second most abundant species in the active community, representing 34% of all individuals collected.

The passive and the active communities

The rarefaction curves show that ostracod richness reached an asymptote in the passive community,

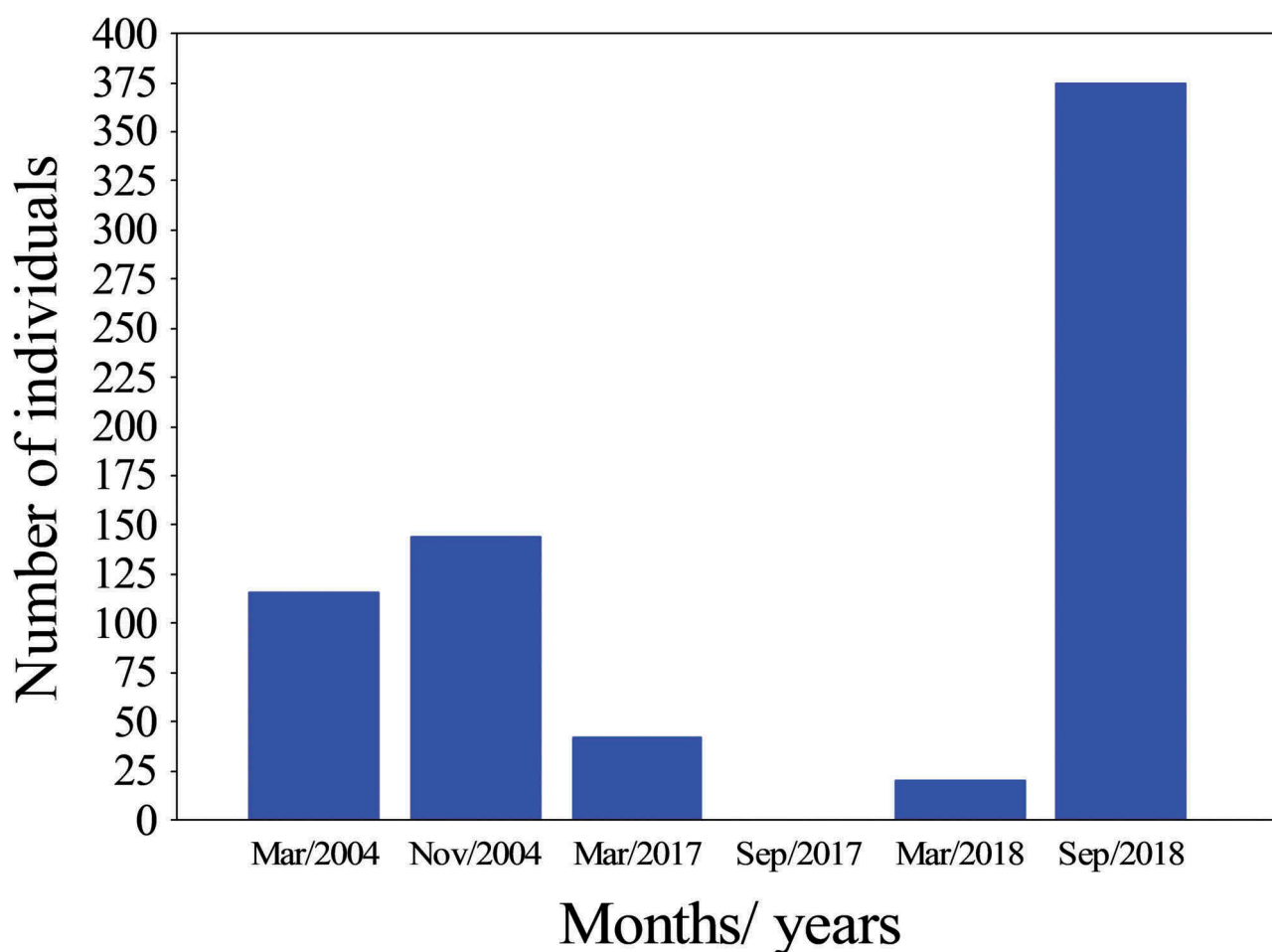


Figure 4. Number of individuals collected from the active community in 2004, 2017, and 2018 in Osmar Lake in the Upper Paraná River floodplain.

while an increasing trend of the richness was observed in the active community. The active community had a higher number of species for the same number of individuals (Figure 5). However, we did not observe significant differences in richness (Welch t-test $t = 0.72$, $df = 5.90$, $p = 0.28$), nor in abundance (Welch t-test $t = -1.18$, $df = 5.98$, $p = 0.70$) between the passive and active communities.

The species composition between active and passive communities was significantly different (Pseudo- $F = 5.41$, $p = 0.003$) (Figure 6). Only four species, *C. iheringi*, *Cypridopsis* cf. *vidua*, *D. meridana*, and *S. bicuspis* were common in both communities (Table 1).

No significant differences ($F = 0.14$, $p = 0.90$) were found in the variability of ostracod species composition between active and passive communities. However, the average distance to the centroid was higher in the active community (0.462) as compared to the passive community (0.452).

Discussion

The passive community

The eight ostracod species that hatched from the egg banks all belong to the family Cyprididae. Most species of the Cyprididae can produce drought-resistant eggs (Horne & Martens 1998), so this is not a real surprise. The strategy to produce drought-resistant stages, together with the ability to reproduce parthenogenetically and the ability to swim, are largely the causes of the evolutionary success of this family (Horne & Martens 1998), which comprises about half of all extant non-marine ostracod species (Meisch et al. 2019). The production of drought-resistant eggs allows for survival in temporary habitats and also facilitates passive dispersal of these organisms by biotic and abiotic vectors, especially in combination with parthenogenetic reproduction in which one egg can be sufficient to establish a new population (Brochet et al. 2010). An example of

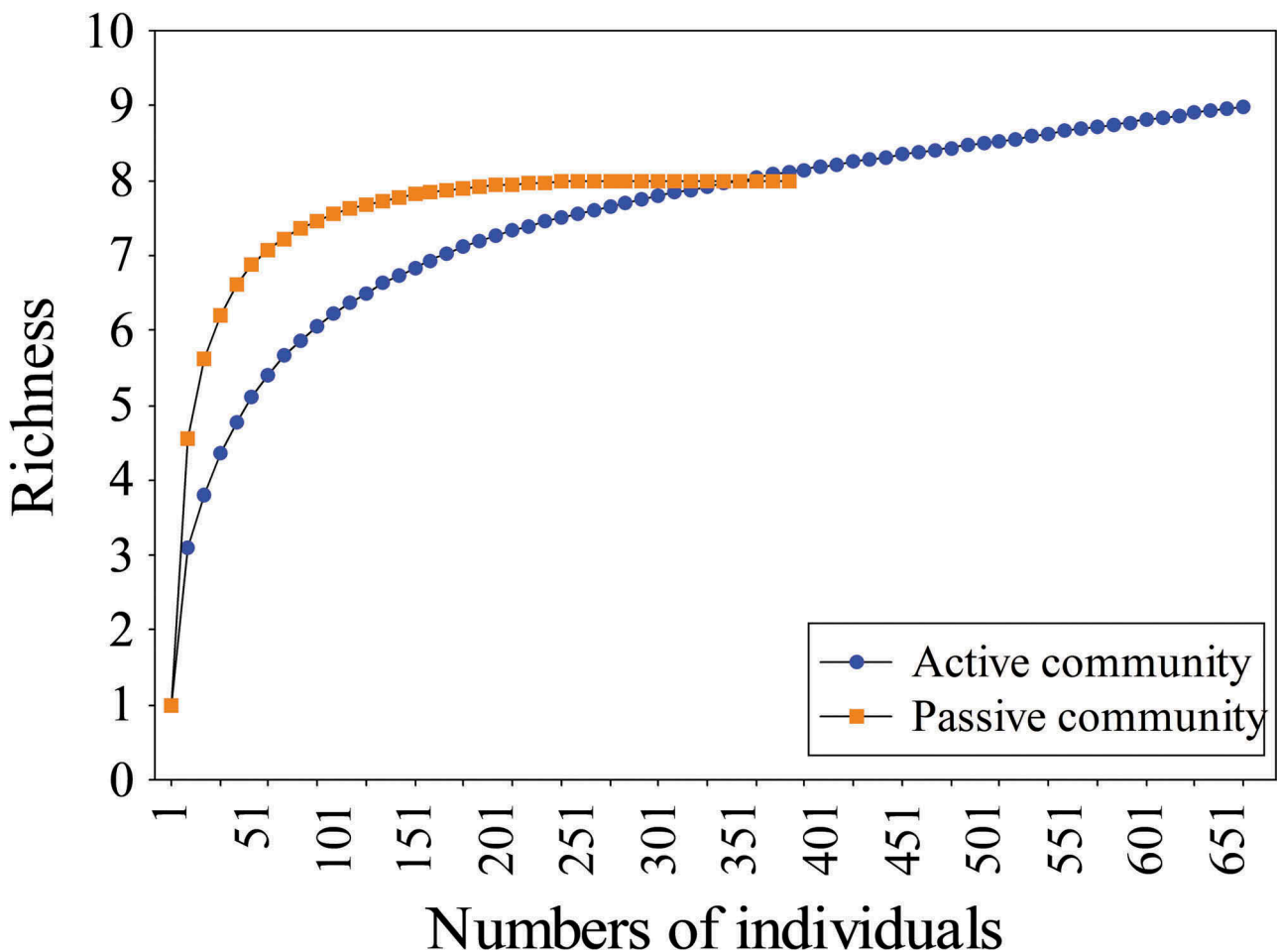


Figure 5. Rarefaction curves of the active and passive communities of ostracods from Osmar Lake in the Upper Paraná River floodplain.

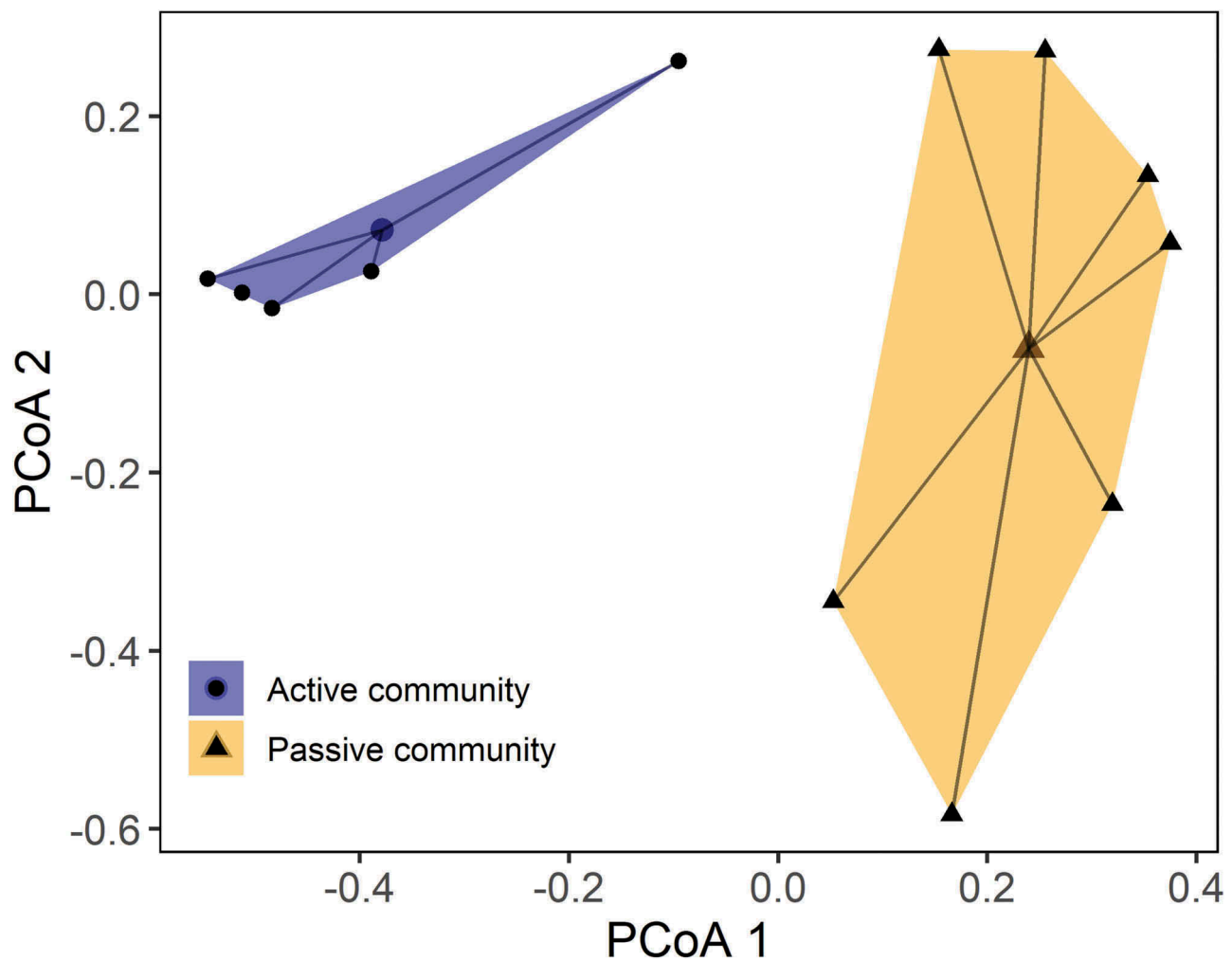


Figure 6. Principal coordinate analysis showing the variability in the ostracod species composition in both active and passive communities from Osmar Lake in the Upper Paraná River floodplain.

an invasive ostracod species from South America is *Strandesia bicuspis*, one of the most abundant species in the passive community in the present study, which was introduced in Europe by ornamental aquatic plants (Matzke-Karasch et al. 2014).

The high richness and abundance of the passive ostracod community in this temporary lake (Osmar Lake) are in agreement with the findings of Palazzo et al. (2008b) and Stenert et al. (2017). These authors showed that drought periods and hydrodynamic stress, by reducing connectivity between the environments, seem to cause higher richness of zooplankton and cladocerans, respectively.

The egg banks of Osmar Lake may contain eggs of species that accumulated over several generations and seasons, owing to the recurrent wet/drought oscillations (Bertoncin et al. 2019). However, four of the eight ostracod species which hatched from the egg bank were not recorded in the active community in this temporary lake, reflecting the ‘ecological memory’ of this environment.

The eggs of these species might have been carried into this lake during flooding or were produced by past active populations in the lake or might have accumulated in the sediments by a combination of both of these mechanisms. Even though these four species were not found in the active community during the present study, they most likely appeared in the past and might do so again in the future. Thus, events that occurred in the past can influence and shape present or future communities through the set of species that remain dormant in the sediment (Padišák 1992). It is therefore important to consider the passive community in biodiversity studies, especially those in conservation areas, since this passive community can hold species not found in the active community, thus providing more accurate diversity estimates. Gerhard et al. (2017) suggested that egg banks can provide a good picture of the environment without historical information and when financial resources are limited to cover new sampling campaigns.

The active community

Osmar Lake has been the focus of long-term research encompassing several aquatic communities. Mormul et al. (2012) showed that there are different ecological states possible in this lake, from turbid to clear-water conditions, and associated the clear water phase with migration of benthic fish out of the lake, together with the establishment of submerged plants during the period of rising water levels. This condition might have contributed to the establishment of the active community of ostracods in March 2004, 2017, 2018, and November 2004 (rainy season), owing to decreased predation by fish and increased availability of macrophytes. No ostracods were recorded in September 2017 (dry season), when the lake was in a turbid state and there was a high biomass of benthic fish during this period of low water level (Mormul et al. 2012). As there are species of fish (e.g. *Hyphessobrycon eques* (Steindachner, 1882)) in the lake that feed on ostracods (Crippa et al. 2009), ostracod communities could be depleted during such stages of the ecosystem, ostracod communities could be depleted during such stages of the ecosystem. The predation pressure combined with the absence of the macrophytes which provides substrate and shelter for ostracods could drive active ostracod communities into local extension, even before the complete desiccation of the lake. In addition, low water levels and high decomposition during the dry period might reduce oxygen concentrations (Williams 2006), which can make the environment hypoxic, thus reducing the presence of ostracods in September 2017. There was a period of long drought in 2018 and rainfall was recorded few days prior to the collection. This rain formed small pools in the lake body and thus might have stimulated the hatching of eggs. This might have contributed to the large numbers of individuals from different species of ostracods recorded in September 2018.

Cytheridella ilosvayi is generally common and abundant in aquatic environments of the Upper Paraná River floodplain (Higuti et al. 2017), mainly in isolated lakes (Conceição et al. 2017), and was the second most common species in the present study. *Cytheridella ilosvayi* is a brooder species and eggs and the first two or three juvenile stages are retained within the brood chambers until they are released from the carapace. The other species recorded from this temporary lake are not brooders. This brooding strategy could ensure the survival of the offspring for a moderate period of time, keeping the eggs and juveniles inside the carapace (Smith et al. 2015), while the sediment of the lake remains moist. However, it is highly unlikely that animals and juveniles can survive fully desiccated conditions over several months in such a state of torpidity. In addition, *C. ilosvayi* does not produce drought-

resistant stages. We must therefore accept that *C. ilosvayi* is re-introduced by flooding after each drought period.

Biotic and abiotic dispersal in floodplains is indeed a factor that should be considered in the structuring of the active community of floodplain lakes (Brochet et al. 2010). Osmar Lake is an environment adjacent to the Paraná River, and the water level fluctuations in the lake are strongly influenced by the hydrological dynamics of the main river channel (Mormul et al. 2012). Dispersal of ostracods in floodplains can occur mainly in pleuston, the associated biota living in the root systems of free-floating aquatic macrophytes, which are especially common in Neotropical floodplains. Such floating macrophytes can enter into adjacent areas and biotopes such as Osmar Lake when the water level of the Paraná River exceeds 350 cm and overflows into the lakes (Souza Filho 2009). Ostracods have a strong association with the roots of such plants, which serve to them as a substrate for living, sheltering, feeding, and reproducing (Higuti et al. 2010; Matsuda et al. 2015).

It is worth noting that there is a narrow channel that connects Osmar Lake with the main channel of the Paraná River. This connection between river, channel, and lake is inundated when the Paraná River is 1 m above a marginal dike. This channel can serve as a dispersion route for plankton, macrophytes, and fish during flood periods and as a source of input for allochthonous material. The lateral connectivity and water flow between aquatic environments tend to homogenize communities in floodplains (Amoros & Bornette 2002) and is important for the life cycle of some invertebrates as it provides the necessary conditions for development (Amoros & Bornette 2002).

The dispersal of species of Candonidae can also occur through drifting plants during flooding. Apart from that, some Candonidae species may inhabit the hyporheic zone and species could use this environment as refuge during drought (Dole-Olivier et al. 2000). However, the existence of this type of refugia is as yet speculative, because we did not sample the hyporheic zone in the present study.

The passive and the active communities

Our results show that the passive community is capable of harboring high numbers of ostracod species and individuals, although the differences in the richness and abundance with the active community were not significant. Martens et al. (1992) on a temporary pool in Israel and Havel et al. (2000) in lakes of the USA also observed

higher numbers of ostracod species in the passive community, as compared to the active community. Both these studies have shown differences in species composition between passive and active communities and the existence of species occurring exclusively in the passive community (Martens et al. 1992; Havel et al. 2000). We here show the same for the ostracod community of the temporary Osmar Lake in the Paraná River floodplain. The overwhelming abundance of living *C. ilosvayi* and the absence of four Cyprididae species from the active community, which were present in the passive community, is especially puzzling if we compare the reproductive strategies of these species. *Cytheridella ilosvayi* is considered a K-strategist species, with sexual reproduction and parental care, where females carry the offspring and eggs into the brood chambers, causing a limited number of offspring per female (Horne & Martens 1998). In contrast, the Cyprididae species recorded in the egg bank are considered r-strategists, since their reproduction is mostly asexual, and they generally produce large amounts of resting eggs (Horne & Martens 1998). Based on this, we could expect that these Cyprididae would easily outcompete *C. ilosvayi* in the active community, but it appears that the opposite is the case. During the present study, no specimens of Candonidae hatched from the passive community. This indicates that also *Candobrasilopsis brasiliensis*, *Candobrasilopsis rochai*, *Pseudocandona agostinhoi*, and *Cytheridella ilosvayi*, although present in the active community, are probably allochthonous species that are repeatedly introduced into the lake through flooding in floating macrophytes. Swimming Cyprididae species are abundant in the passive community and can occur in the active community during flooding, when the conditions are favorable for resting egg hatching and when fish predation is reduced or absent.

When performing biodiversity surveys in areas such as floodplains, where fluctuating water levels can cause the existence of temporary habitats, it is important to investigate both active and passive communities to assess the total biodiversity. This is especially important for monitoring programs on the conservation and management of temporary aquatic environment. Both short and long-term research are important to understand the inter-annual dynamics of temporary floodplain lakes because with climate change, extreme drought events could become more frequent and could last longer. This could have effects on the dynamics of meta-communities (Campos et al. 2019), on biodiversity in general and on ecosystem functioning and the resulting ecosystem services. The present research also shows that it is highly necessary to test the relevance of allochthonous introductions in temporary floodplain lakes because their influx

can strongly influence the structure and species composition of both passive and active communities.

In conclusion, the egg banks can add species not necessarily found in the active community, thus acting in the maintenance and enrichment of both local and regional biodiversity.

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