



Effects of spatial scale and habitat on the diversity of diapausing wetland invertebrates

Raquel Fontoura Freiry¹, Fernanda Mara Esquinatti¹, Cristina Stenert¹,
Alexandre Arenzon², Daryl L. Nielsen³, Leonardo Maltchik^{1,*}

¹Laboratory of Ecology and Conservation of Aquatic Ecosystems, University of Vale do Rio dos Sinos (UNISINOS), 93022-000 São Leopoldo, RS, Brazil

²Laboratory of Ecotoxicology, Ecology Center, Federal University of Rio Grande do Sul, 91501-970 Porto Alegre, RS, Brazil

³The Murray-Darling Freshwater Research Centre, CSIRO Land and Water Flagship and La Trobe University, Wodonga, University Drive, VIC 3690, Australia

ABSTRACT: The community structure of aquatic invertebrates producing dormant propagules has been associated with both local and regional-scale factors in temporary wetlands. We explore how patterns in the diversity of drought-resistant aquatic invertebrates are related to different spatial scales in ponds with distinct plant structural complexities. We tested 3 hypotheses: (1) the finest spatial scale (fine-scale diversity) has the strongest contribution to diversity and composition; (2) the fine-scale diversity will be higher in habitats that are more complex; and (3) the habitat-scale diversity has a higher contribution to regional diversity than broad- and fine-scale diversity. Dry sediment samples were collected from 3 ponds with 2 distinct plant habitats. The findings from individual partitions show that the importance of spatial scales was different between habitats. Fine-scale diversity represented a greater fraction of the total diversity for the habitat with the highest complexity, and broad-scale diversity showed a substantial contribution to total diversity in the habitat with the lowest complexity. Habitat-scale diversity contributed most to regional diversity, which underlines the importance of habitat type in the diversity of aquatic invertebrates that produce dormant propagules in temporary ponds.

KEY WORDS: Additive partitioning · Plant complexity · Dormancy · Egg bank · Temporary pond · Microcrustacean

INTRODUCTION

Wetlands are highly productive and support a rich biodiversity harboring many species with behavioral and physiological adaptations to endure hydrological fluctuations (Williams 2006). Dormancy during dry periods is a common solution to invertebrate survival and persistence in most temporary wetlands (Williams 1998), and dormant stages can remain viable in dry sediments for many years (De Stasio 1990). Invertebrate resting stages also provide a means of maintaining genetic, phenotypic, species and community diversity during unfavorable dry periods (Hairston 1996, Brendonck & De Meester

2003, Santangelo 2009), and as a consequence of their longevity, they integrate spatial and temporal variations in community composition, which confers a measure of community resilience to adverse conditions (Brock et al. 2003).

Wetland ecosystems typically have high macrophyte diversity (Cronk & Fennessy 2001) resulting in highly heterogeneous and structurally complex habitats (Mormul et al. 2011). Habitat complexity of wetlands results from distinct habitats of dominant vegetation types (e.g. submerged, emergent, floating) that directly affect the occurrence and distribution of aquatic invertebrates (Cheruvilil et al. 2000, 2002, Thomaz et al. 2008, Dibble & Thomaz 2009). The

*Corresponding author: maltchik@unisinis.br

structural complexity generated by aquatic plants provides refuge for invertebrates, making them less vulnerable to predation, and also suitable breeding and foraging substrates (Gilinsky 1984). Therefore, invertebrate diversity and abundance are often positively correlated with the structural complexity provided by different wetland macrophyte species (Stenert et al. 2008, Thomaz & Cunha 2010, Lucena-Moya & Duggan 2011, Mormul et al. 2011).

Aquatic invertebrate communities are structured by processes prevailing at multiple spatial scales (Minshall 1988, Poff 1997, Heino et al. 2003, Ligeiro et al. 2010). The relationship between invertebrate diversity and macrophyte complexity can change among different spatial scales (Thomaz & Cunha 2010). For example, at finer spatial scales (e.g. among macrophyte beds of a small lake or even plants located close to each other), the invertebrate density and diversity varies depending on plant structural complexity (McAbendroth et al. 2005, Thomaz et al. 2008). At a fine scale, the distribution patterns of invertebrates in wetlands has been linked to biotic interactions, habitat heterogeneity and complexity, surface area, hydroperiod, and nutrient concentration (Heino 2000, Tarr et al. 2005, Mormul et al. 2011). Although aquatic ecosystems with different levels of complexity can present distinct patterns of species spatial distribution (Taniguchi & Tokeshi 2004), most studies that have addressed the importance of habitat complexity in diversity were developed on a single spatial scale related to local variables.

The additive partitioning of species diversity is a promising approach to identify the most important sources of biologic diversity in a sampling design of nested spatial scales (Godfray & Lawton 2001). Whittaker (1960, 1972) suggested that biological diversity can be divided into 3 components: alpha (local diversity), beta (variation among sites) and gamma (regional diversity). Lande (1996) and Crist et al. (2003) applied the diversity terms of Whittaker to the additive partition approach, where gamma diversity is obtained by summing the alpha and beta diversities. Since the ecological patterns of a community in a small spatial scale (local) might be different from those observed over broader spatial scales (landscapes or regions) (Crist et al. 2003, Heino et al. 2003), partitioning diversity allows the identification of spatial scales associated with the highest variation in species composition. Recently, the additive partitioning of diversity was used to test scale-dependent patterns of macroinvertebrate diversity in streams (Ligeiro et al. 2010) and coastal wetlands (Ávila et al. 2011) and demonstrated strong evidence of scale

dependence on diversity partitioning of macroinvertebrate communities, with beta diversity at the broad spatial scale making a large contribution to total diversity.

In temporary wetlands, the relationship between invertebrate propagule banks and macrophyte complexity over different spatial scales has not been investigated, although it has been demonstrated that differences in the community structure of dormant propagules is associated with both local and regional-scale factors (Angeler et al. 2008, Fernández et al. 2009). In this study, we explore how patterns in the diversity and composition of drought-resistant aquatic invertebrates are related to different spatial scales (sediment cores, plant habitats and ponds) in ponds with distinct plant structural complexities. We used the additive partitioning approach to test 3 hypotheses: (1) the finest spatial scale (fine-scale diversity) has the strongest contribution to diversity and composition of drought-resistant aquatic invertebrates due to their poor active dispersal capacity (Fernández et al. 2009); (2) the fine-scale diversity will be higher in habitats that are more complex, where higher plant structural complexity increases the invertebrate diversity (Thomaz et al. 2008, Dibble & Thomaz 2009); and (3) the habitat-scale diversity has a higher contribution to regional invertebrate diversity than the broad and fine scales, since the invertebrate diversity and composition changes among macrophyte beds of a same small pond, depending on plant structural complexity (McAbendroth et al. 2005, Thomaz et al. 2008).

MATERIALS AND METHODS

Study area

The study was conducted in Bom Jesus county (28° 40' 04" S, 50° 25' 00" W), located in the Planalto Superior of Rio Grande do Sul, southern Brazil, an area known as altitude fields ('Campos de Cima da Serra') (altitude ~1200 m). The study area vegetation comprises natural pastures with dominance of natural grasslands and patches of mixed ombrophyllous forest (Araucaria forest). The altitude fields are located in the southern portion of the Mata Atlântica Biome. The wetlands of altitude fields are typically small (1–3 ha) and strongly affected by precipitation and evaporation. The climate is classified as super humid temperate. The mean annual temperature is 14.5°C, but sub-freezing temperatures may occur from April to November (Backes 1999). The mean annual

rainfall varies from 1500 to 1700 mm, without a marked dry season (Bond-Buckup et al. 2010).

Experimental design

In the austral summer of 2014, 3 natural temporary ponds were selected, in each of which 2 distinct dominant plant habitats with differing structural complexity occurred: stands of Peruvian watergrass *Luziola peruviana*, characterized as the 'habitat with the lowest complexity', and *Sphagnum* bog, characterized as the 'habitat with the highest complexity'. *Sphagnum* bog is dominated by a dense growth of *Sphagnum* sp. moss, which forms a heterogenic and architecturally denser and more complex habitat compared with Peruvian watergrass habitat (Kuczyńska-Kippen 2008). The minimum area occupied by each distinct plant habitat was approximately 30% of the total area of each pond. All ponds had similar areas (~1 ha), water depth (~0.4 m) and hydroperiods (~6 mo with surface water in a year). Ponds were located from 3 to 10 km from each other.

Sampling was hierarchical and included sediment cores, habitats and ponds (Fig. 1). Within each pond, 3 random cores were taken from each of the 2 habitats (6 samples per pond) (Fig. 1). We used modified methods by Ávila et al. (2015) and Stenert et al.

(2016). In brief, dry sediment sampled per habitat in each pond was homogenized and distributed into plastic trays, totaling 18 trays (3 samples \times 2 habitats \times 3 ponds). In an experimental room, the trays were flooded with distilled water and stored at constant temperature and photoperiod over 21 d. Aquatic invertebrates were sampled on Days 2, 7, 14 and 21. Three sweeps were performed in each tray and the sampled invertebrates were preserved with 80% ethanol (Ávila et al. 2015, Stenert et al. 2016) and identified to species level (cladocerans) and lower taxonomic resolutions (ostracods and copepods) according to Elmoor-Loureiro (1997). The invertebrates were deposited in the Laboratory of Ecology and Conservation of Aquatic Ecosystems of University of Vale do Rio dos Sinos (UNISINOS).

Data analysis

Invertebrate richness was compared between the 2 habitats over time (using ponds as replicates) using repeated-measures ANOVA. Where significant differences between habitats were indicated, Tukey tests were applied *a posteriori* for multiple comparisons among the different days after initial sediment rehydration. Richness data were transformed to square root prior to statistical analyses to ensure normality of the data set and equality of variances. The Levene's test verified the homogeneity of variance assumption, and the Mauchly's test of sphericity verified the sphericity assumption. Assuming compound symmetry (homogeneity of the variance-covariance matrix), no adjustment was made for the *F*-test. Analyses were performed using SPSS software, version 18.0 (SPSS 2009).

Non-metric multidimensional scaling analysis (NMDS) was used to assess the variation in invertebrate community composition between the 2 habitats throughout the experiment (Clarke & Warwick 1994). This analysis was performed with the Sorensen distance matrix (presence and absence data) using 2 axes in the R statistical program (R Development Core Team 2009). A 2-way permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001) was used to compare differences in the community composition between the 2 habitats over time (habitat effect + time effect + habitat \times time interaction effect). We used the Sorensen distance matrix and 9999 permutations to validate the model significance. The analyses were carried out using the vegan package (Oksanen et al. 2009) in the statistical software R version 2.9.0 (R Development Core Team 2009).

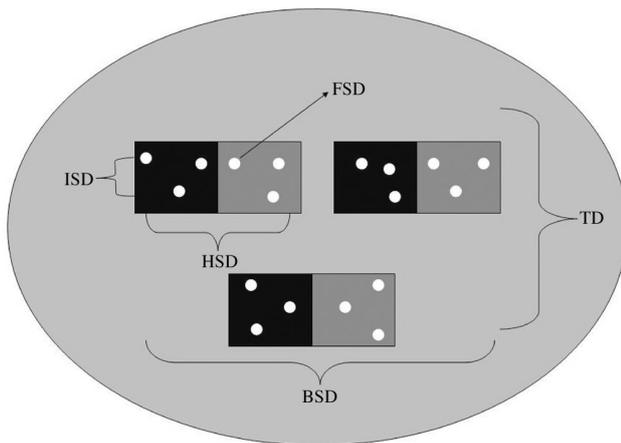


Fig. 1. Schematic representation of sampling design and diversity partitioning among and within the 3 ponds. Fine-scale diversity (FSD) = mean invertebrate richness per individual core; intermediate-scale diversity (ISD) = differences of invertebrate taxa between cores; habitat-scale diversity (HSD) = differences of invertebrate taxa between habitats; broad-scale diversity (BSD) = differences of invertebrate taxa between ponds; TD = total diversity. Black squares represent the habitat with the highest plant complexity and grey squares represent the habitat with the lowest plant complexity

Additive partitioning of diversity was used to decompose the total variation in community composition (regional diversity) into different spatial scales of diversity. In our study, individual rehydrated cores represent our basic units. The invertebrate diversity was analyzed at 3 different spatial scales: (1) the finest spatial scale was the location-induced diversity and corresponded to the individual cores in each habitat ($n = 18$); (2) the intermediate spatial scale was the plant-community-induced diversity and corresponded to the 3 cores collected in each habitat ($n = 9$); and (3) the broader spatial scale was the pond-induced diversity and corresponded to the individual ponds ($n = 3$) (Fig. 1). Therefore, the total diversity was partitioned into the average diversity (expressed as a percentage) within individual rehydrated cores, defined as the average richness per basic unit (fine-scale diversity), between rehydrated cores (represented by the differences of invertebrate taxa collected in the basic units (intermediate-scale diversity) and between ponds (broad-scale diversity).

Partition analyses were performed to compare the relative contribution of each spatial scale between the habitats with the lowest and highest plant complexities. For this, the data were analyzed separately for each plant habitat. A partition analysis was also performed to verify the habitat-scale diversity contri-

bution compared with the other spatial scales (Fig. 1). The additive partition analyses were performed using PARTITION version 3.0 (Veech & Crist 2007), and the statistical procedures are detailed by Ávila et al. (2015). Since the samples at the highest spatial scale (ponds) contain the same number of samples at the habitat spatial scale, the sampling design was balanced in the analyses.

RESULTS

A total of 3312 individuals from 14 taxa were collected over the experiment. All invertebrates that emerged from dormant propagules were microcrustaceans. Dominant microcrustaceans were cladoceran species, which were represented by 3043 individuals and 12 species. The most abundant cladoceran species were *Macrothrix elegans* and *Ilyocryptus spinifer*, representing 46 and 26% of the individuals sampled, respectively. *Kurzia polypina* and *Chydorus eurynotus* were the most abundant species of chydorids. Calanoid copepods and ostracods were also found over the experiment (Table 1).

The timing of emergence of the invertebrate species varied between the habitats with the lowest and highest complexity over the experiment. The first

Table 1. Total numbers of drought-resistant aquatic invertebrates that emerged from habitats with the lowest and highest plant complexity in pond sediments of southern Brazil following rehydration (Days 2, 7, 14 and 21)

Taxa	Highest plant complexity				Lowest plant complexity				Total abundance
	2	7	14	21	2	7	14	21	
Cladocera									
<i>Alona ossiani</i>	0	0	4	6	0	0	0	1	11
<i>Camptocercus similis</i>	0	1	3	15	0	0	2	16	37
<i>Ceriodaphnia silvestrii</i>	0	3	0	10	0	0	0	1	14
<i>Chydorus eurynotus</i>	0	1	5	143	0	0	1	3	153
<i>Ephemeroporus tridentatus</i>	0	0	6	10	0	1	2	9	28
<i>Ilyocryptus spinifer</i>	10	43	69	304	0	10	53	289	778
<i>Karualona muelleri</i>	0	0	4	24	0	0	1	1	30
<i>Kurzia polypina</i>	0	1	30	134	0	0	0	2	167
<i>Leberis davidi</i>	0	12	2	3	1	0	2	3	23
<i>Macrothrix elegans</i>	4	80	137	869	0	5	34	179	1308
<i>Pseudosida bidentata</i>	9	17	40	138	0	0	0	0	204
<i>Simocephalus serrulatus</i>	1	8	15	245	0	1	0	20	290
Calanoids	0	111	95	60	0	0	0	0	266
Ostracods	0	0	0	0	2	0	0	1	3
Total richness	4	10	12	13	2	4	7	12	14
Total abundance	24	277	410	1961	3	17	95	525	3312

Table 2. Results of ANOVA and PERMANOVA tests for the effects of habitat, time and the interaction between habitat and time on the invertebrate richness and composition in altitude ponds in southern Brazil

Dependent	Independent	df	SS	MS	F	p
Richness	Habitat	1	11.221	11.221	9.238	0.038
	Residual	4	4.859	1.215		
	Time	3	8.456	2.819	6.391	0.008
	Habitat × Time	3	0.661	0.220	0.499	0.690
	Residual	12	5.293	0.441		
Composition	Habitat	1	0.698	0.698	5.328	0.001
	Time	3	0.640	0.213	1.628	0.129
	Habitat × Time	3	0.691	0.230	1.758	0.122
	Residual	11	1.441	0.131		

taxa that emerged from sediments of the habitat with the lowest plant complexity were *Leberis davidi* and the ostracods (48 h of sediment re-wetting), and the species that emerged late were *Ceriodaphnia silvestris*, *K. polyspina* and *Alona ossiani* (21 d of sediment re-wetting). In the habitat with the highest plant complexity, 4 species emerged after the first 48 h (*I. spinifer*, *Simocephalus serrulatus*, *M. elegans*, and *Pseudosida bidentata*). All taxa found in the habitat with the highest complexity emerged within the first 14 d of sediment re-wetting. *P. bidentata* and calanoids emerged only in the habitat with the highest plant complexity. The most abundant species were *I. spinifer* and *M. elegans* for both pond habitats.

The invertebrate richness was higher in the habitat with the highest plant complexity over the experiment ($F_{1,4} = 9.238$; $p = 0.038$) (Table 2, Fig. 2). The richness also changed over the duration of the experiment ($F_{3,12} = 6.391$, $p = 0.008$), and it was higher after 21 d of sediment re-wetting than in the first week (2 and 7 d

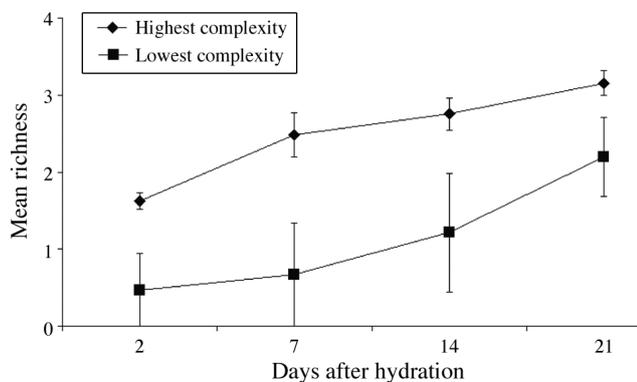


Fig. 2. Invertebrate richness (mean \pm SE) of dormant propagules of aquatic invertebrates in altitude ponds in southern Brazil over the experiment in habitats with the lowest and highest plant complexity following the dry sediment hydration

after re-wetting) ($p < 0.05$). No interaction between habitat and time was observed in invertebrate richness ($F_{3,12} = 0.499$, $p = 0.690$) (Table 2, Fig. 2).

The dissimilarity of invertebrate composition between the habitats with the lowest and highest plant complexity over the experiment was represented by 2 axes of the NMDS ordination (stress = 0.09) (Fig. 3). The composition of the communities that emerged from propagule banks differed between the habitats with the lowest and highest plant complexity ($F_{1,11} = 5.328$; $p = 0.001$). However, the composition did not change over the

experiment ($F_{3,11} = 1.628$; $p = 0.129$). No interaction between habitat and time was observed in invertebrate composition ($F_{3,11} = 1.758$; $p = 0.122$), showing that the composition variation between habitats was independent of time (Table 2).

Partitioning of invertebrate diversity showed similar patterns for both pond habitats. The fine-scale diversity was lower than expected from the null

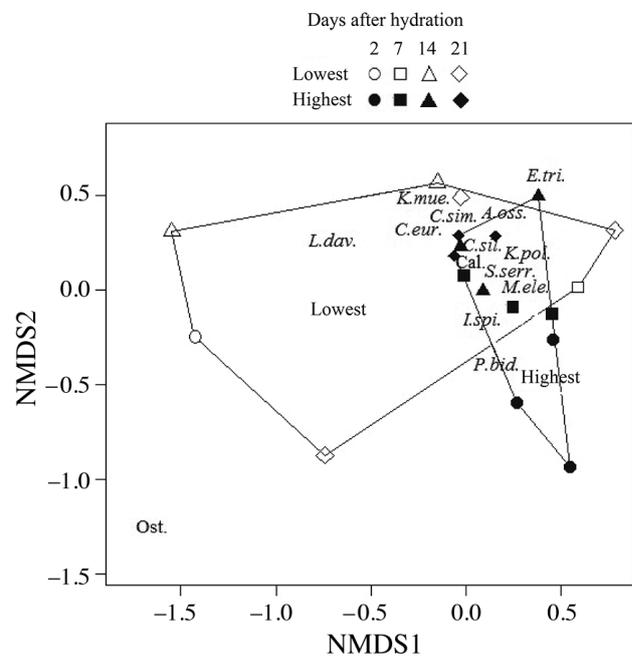


Fig. 3. NMDS ordination diagram of aquatic invertebrate taxa found in habitats with the lowest and highest plant complexity (stress: 0.09). *A.oss.*: *Alona ossiani*; *C.eur.*: *Chydorus eurynotus*; *C.sil.*: *Ceriodaphnia silvestris*; *C.sim.*: *Camptocercus similis*; *E.tri.*: *Ephemeropterus tridentatus*; *K.mue.*: *Karualona muelleri*; *K.pol.*: *Kurzia polyspina*; *I.spi.*: *Ilyocripton spinifer*; *L.dav.*: *Leberis davidi*; *M.ele.*: *Macrothrix elegans*; *P.bid.*: *Pseudosida bidentata*; *S.ser.*: *Simocephalus serrulatus*, Cal.: Calanoid, Ost.: Ostracoda

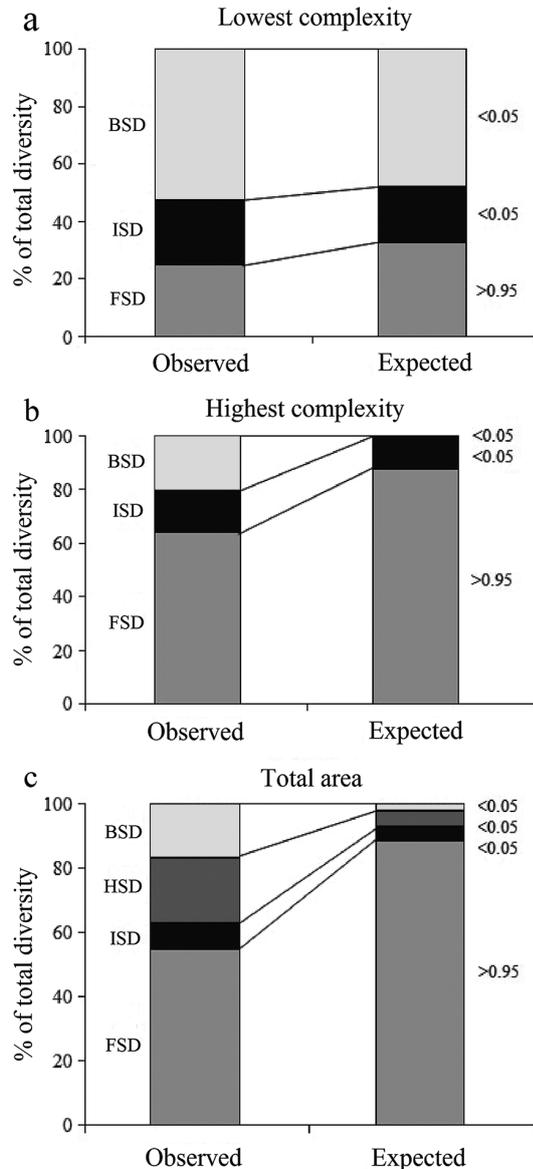


Fig. 4. Observed and expected diversity, partitioned into different spatial scales of diversity, expressed as percentage of total richness in (a) habitat with the lowest complexity, (b) habitat with the highest complexity and (c) total area. For individual partitions per habitat (a and b). See Fig. 1 for abbreviations and description of diversity scales. The numbers indicate the proportion of expected samples containing more species than the observed sample for each partition

model ($p > 0.95$), but the intermediate and broad scales of diversity were higher than expected from the null model ($p < 0.05$) (Fig. 4a,b). The fine-scale diversity represented a greater fraction of the total diversity for the habitat with the highest complexity (64.08%). However, in the habitat with the lowest complexity, this spatial scale represented a smaller fraction of the total diversity (25%). The intermediate and broad scales of diversity had different contribu-

tions between pond habitats (habitat with the highest complexity: intermediate-scale diversity = 15.38%, broad-scale diversity = 20.54%; habitat with the lowest complexity: intermediate-scale diversity = 22.25%, broad-scale diversity = 52.75%). The invertebrate diversity and composition variations between ponds (broad-scale diversity) were higher in the habitat with the lowest complexity than in the habitat with the highest complexity (Figs. 3 & 4a,b). These results showed that the differences of invertebrate taxa might change depending on the scale of study in different habitat types.

The results of the second partition analysis—including the habitat type as an additional level in the hierarchical design—showed that while the fine-scale diversity was lower than expected under the null model ($p > 0.95$), the other scales of invertebrate diversity (intermediate, habitat and pond scales) were significantly higher than expected from the null model ($p < 0.05$) (Fig. 4c). In relation to the contribution from each spatial scale for total diversity, the fine-scale diversity was higher than the other diversity scales, representing the greatest fraction of the total invertebrate diversity (54.79%), followed by the habitat scale (20.07%) and the pond scale (17.07%). The intermediate-scale diversity represented the lowest contribution to total diversity (8.07%) (Fig. 4c).

DISCUSSION

Our results showed that the fine-scale diversity was lower than expected from the null model for both habitats, thus indicating high aggregation among invertebrates at fine spatial scales. This pattern may be related to the poor active dispersal capacity of drought-resistant aquatic invertebrates (Hairston 1996, Fernández et al. 2009), and also to the concentrated deposition of eggs in the sediment, reaching thousands of eggs per m^2 (Santangelo 2009). A similar result has been demonstrated for zooplankton communities of tropical rivers during drought and flooding periods (Melo & Medeiros 2013).

Our first hypothesis—the finest spatial scale contributed most to the diversity and composition of drought-resistant aquatic invertebrates—was partially accepted because the importance of this particular spatial scale varied between habitats. The fine-scale diversity was higher in the habitat with the highest complexity, where higher plant structural complexity provides a variety of microhabitats, thus creating more available ecological niches for associated animals (Warfe & Barmuta 2004, Hansen et al.

2011). On a fine spatial scale, a high plant complexity can increase the aquatic invertebrate diversity (Thomaz & Cunha 2010). In the habitat with the lowest complexity, the fine-scale diversity represented a smaller fraction of the total diversity compared with the broad-scale diversity. These results supported our second hypothesis i.e. that the fine-scale diversity contributed more to the total invertebrate diversity in the habitat with the highest plant complexity.

Our third hypothesis was refuted since the habitat-scale diversity had a similar contribution to regional invertebrate diversity compared with the broad spatial scale, and a lower contribution than the fine scale. However, this study clearly indicates that more complex habitats do not only harbor a higher diversity of invertebrates, but also contribute to the recovery of communities from dormant propagules more efficiently than less complex habitats. Other studies also observed a positive relationship between habitat complexity and species diversity (Thomaz et al. 2008, Hansen et al. 2011, Mormul et al. 2011, Choi et al. 2015). Kuczyńska-Kippen (2008) found that more diverse and abundant zooplankton communities occurred in the *Sphagnum* mat in relation to the open-water zone in a lake of northern Poland. Henrikson (1993) demonstrated that *Sphagnum* bogs supported a 10-fold increase in Cladocera abundance compared with less complex habitats. Not only are *Sphagnum* bogs more structurally complex, they are habitats subject to prolonged water saturation (Silva 2002) and allow for longer flooded periods and refuge creation for aquatic invertebrates.

The ability of the dormant propagules to rapidly respond to rehydration was observed in this study. A fast emergence response of dormant propagules is an important characteristic of aquatic invertebrates in intermittent wetlands (Golladay et al. 1997), and a response of invertebrates within 48 h of re-wetting has been previously reported (Boulton & Lloyd 1992, Nielsen et al. 2000, Brock et al. 2003, Williams 2006, Ávila et al. 2015). However, the timing of invertebrate emergence varied between the species of the habitats with the lowest and highest complexity. In the habitat with the highest complexity, *Ilyocryptus spinifer*, *Macrothrix elegans*, *Simocephalus serrulatus* and *Pseudosida bidentata* emerged in the initial 48 h after the sediment rehydration; in the habitat with the lowest complexity, only *Leberis davidi* and ostracods emerged in the same period. The hatching dynamics of dormant propagules in the sediment can be influenced by the life history of the species, hatching phenology, and habitat and microhabitat characteristics (Brendonck & De Meester 2003).

Studies using dormant stages are useful for the analysis of wetland diversity since they enable the sampling of a larger number of species than active forms (Mergeay et al. 2006) and also integrate much of the spatial and seasonal variation in the richness, abundance and composition of aquatic invertebrate species (Brendonck & De Meester 2003). Our findings clearly indicated that there was a strong evidence of scaling dependence on diversity partition of aquatic invertebrates that produce dormant propagules. Our study has enabled the identification of the spatial scales that contribute most to the aquatic invertebrate community diversity as well as the influence of habitat structural complexity on community structuring. We believe that future studies in a more extensive area with a large number of ponds are important to further confirm our results.

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