RESEARCH ARTICLE

Macrophyte life forms influence the effects of environmental and spatial factors on the beta-diversity of associated ostracod communities (Crustacea)

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Abstract

Beta-diversity measures have been used to understand patterns of community distribution in natural ecosystems. Recent studies included different facets of beta-diversity analyses, e.g. trait- and phylogeny-based. Here, we used ostracod communities to evaluate the influence of environmental and spatial factors structuring different facets of beta-diversity and their components (Beta-total, replacement and richness-difference) of ostracod communities associated with different macrophyte life forms. We test the hypotheses (1) that the influence of environmental factors is higher for ostracod beta-diversity facets of communities associated with submerged plants compared to emergent and floating plants and (2) that the influence of spatial factors is higher in communities associated with rooted, compared to non-rooted plants. Ostracods were sampled from five life forms of macrophytes, including emergent, rooted floating, rooted submerged, free submerged and free floating in 25 floodplain lakes. Our results showed that the environmental factors turned out to be important for all beta-diversity facets of ostracod communities, mainly for those associated with submerged macrophytes, thus corroborating the first hypothesis. We also found that spatial factors' influence on ostracod beta-diversity was not related to whether the plant is rooted or not, thus refuting our second hypothesis. We also found differences in factors structuring each of the beta-diversity facets, showing the importance to include these three approaches (species-, traits- and phylogeny-based) in ecological surveys. Finally, we highlight the importance of considering different macrophyte life forms in biodiversity surveys for the preservation and management of the diversity of these plants and their associated communities.

Keywords Aquatic plants · Ostracoda · Microcrustaceans · Tropical floodplain · Local and regional factors

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Introduction

Understanding the patterns of community distribution in natural ecosystems, as well as the factors (e.g., local and regional) structuring such patterns, are amongst the main goals of ecological studies (Holyoak et al. 2005). Beta-diversity, which is defined as "the variability in species composition amongst sampling units for a given area" (Anderson et al. 2006), is one of the main concepts that has been used to evaluate such patterns of community distribution (Anderson et al. 2011). Dissimilarities between communities have been attributed to two different process, nl. species replacement or turnover (species are replaced by other species from site to site; Baselga 2010); and richness differences (the gain or loss of species from site to site; Legendre 2014).

In general, studies including beta-diversity measures are based on the taxonomic identity of species (Leibold et al. 2004). However, the communities can be similar in their compositional diversity (based on taxonomic identity of species) and, at the same time, they can differ in their functional and/or phylogenetic diversity (Krasnov et al. 2019), or vice versa (Weinstein et al. 2014). Thus, to overcome this information gap, several authors have measured other aspects of biodiversity, including trait- and phylogenetic-based analyses (Perez Rocha et al. 2018; Alahuhta et al. 2019; Cai et al. 2019; Krasnov et al. 2019). The use of traits helps to understand how species can live, the interaction amongst them, and their contribution to ecosystem functioning (Cadotte et al. 2011). On the other hand, phylogenetic beta-diversity analyses, which measure how phylogenetic relationships amongst species change across space (Graham and Fine 2008), provide information about shared phylogenetic history between two communities (Graham et al. 2009). Besides, this approach helps to identify the ability of communities to generate new evolutionary solutions in the face of environmental changes (Forest et al. 2007). Integrating these different facets in beta-diversity analyses provides complementary and valuable information about community structuring (Alahuhta et al. 2019).

Riverine floodplains are excellent ecosystems to study patterns of community distributions, owing to their wide variety of environments, such as rivers, channels and closed/open lakes, high habitat heterogeneity and high biological diversity (Junk et al. 1989). Aquatic macrophytes are abundant in South American floodplains and they play a role as food resource (Neiff and Casco 2003), in nutrient cycling (Thomaz and Cunha 2010), as a habitat for many organisms, such as fishes (Walker et al. 2013) and associated invertebrates (Rocha and Por 1998; Thomaz and Cunha 2010; Fontanarossa et al. 2013).

Macrophytes have been grouped, according to their life form, in emergent, rooted floating, rooted submerged, free submerged and free floating (Pott and Pott 2000; Souza et al. 2017). Each life form is located in different regions of the water column, mainly related to water characteristics (e.g., chemical and physical variables), leading to different habitat suitability for associated communities (Yamaki and Yamamuro 2013). This variation in environmental characteristics (environmental factors) of the water, for example in temperature, pH, dissolved oxygen and electrical conductivity, are expected to influence the occurrence and structure of associated faunal communities (Nagorskaya and Keyser 2005; Liberto et al. 2012; Mesquita-Joanes et al. 2012). In addition, the influence of spatial factors (e.g., dispersal limitation) is different between aquatic macrophytes, according to their life form (Alahuta and Heino 2013). The efficiency of dispersal might be related to the capacity of the plants to break themselves up (e.g., fixed plants) and regrow from broken dispersed fragments (Bornette and Puijalon 2011) or to detach from the littoral areas of floodplain lakes (e.g., free floating plants), drift in the main channel of rivers and reach other environments (Bulla et al. 2011).

Several studies have evaluated the relationship between the taxonomic identity or structural complexity of the macrophytes (e.g., measured by fractal dimension) and the structure of associated communities (McAbendroth et al. 2005; Matsuda et al. 2015), and it is well-known that the more complex the plant, the higher the diversity of associated animal communities (Thomaz et al. 2008). However, few studies have tested the effects of the different life forms of macrophytes on associated communities (Meerhoff et al. 2003; Cazzanelli et al. 2008; Choi et al. 2014). Thus, the aim of the present study was to evaluate factors affecting the beta-diversity facets (species-, traits- and phylogeny-based) and their components (Beta-total, replacement and richness difference) of ostracod communities associated with macrophytes and to compare these factors amongst different macrophyte life forms. From that, we also assess if the choice of the type of habitat (here: different macrophyte life forms) is an important factor to be considered in studies evaluating beta-diversity of associated animal communities.

We used ostracod (Crustacea) communities, one of the most abundant groups in freshwater ecosystems (Thomaz et al. 2008; Bornette and Puijalon 2011; Liberto et al. 2012; Mazzini et al. 2014; Higuti and Martens 2016; Pereira et al. 2017), associated with five life forms of macrophytes, as a model group. We test two main hypotheses: (1) submerged plants (free submerged and rooted submerged) will have a more pronounced influence on the effects of environmental factors on the beta-diversity of associated ostracod communities than emergent and floating (free floating and rooted floating) plants. This

is expected, because aquatic abiotic variables (e.g. water transparency, dissolved oxygen and water temperature) will have a larger impact on submerged plants, and thus also on associated (animal) communities; (2) the influence of the spatial factors (such as dispersal limitation) on ostracod beta-diversity facets will be higher for fixed (emergent, rooted floating and rooted submerged), compared to non-fixed plants in the sediment (free submerged and free floating). This is based on the expectation that fixed plants have lower dispersal capacity through the region, compared to the unrooted, floating macrophyte life forms. The distribution of ostracod communities associated with these different life forms in macrophytes will thus also be affected by this. Finally, we also test if there are mismatches in the factors (environmental and spatial) structuring each beta-diversity facet (and their components) in each macrophyte life form.

Material and methods

Study site

The Upper Paraná River section is 230 km long and can reach 20 km of width, including several secondary channels and floodplain lakes (Agostinho et al. 2004). It has an extensive floodplain, approximately 60 km long, located within the Brazilian territory (Paraná and Mato Grosso do Sul states). The study area is a river-floodplain system, which encompasses three different river systems: Ivinhema, Paraná and Baía, each one with its peculiar geology, hydrology and limnology (Souza Filho 2009) (Electronic Supplementary Material, Table S1). We selected 25 permanently connected lakes along the Upper Paraná River floodplain, with eight lakes in the Ivinhema system, eight lakes in the Baía system and nine lakes in the Paraná system (Fig. 1).
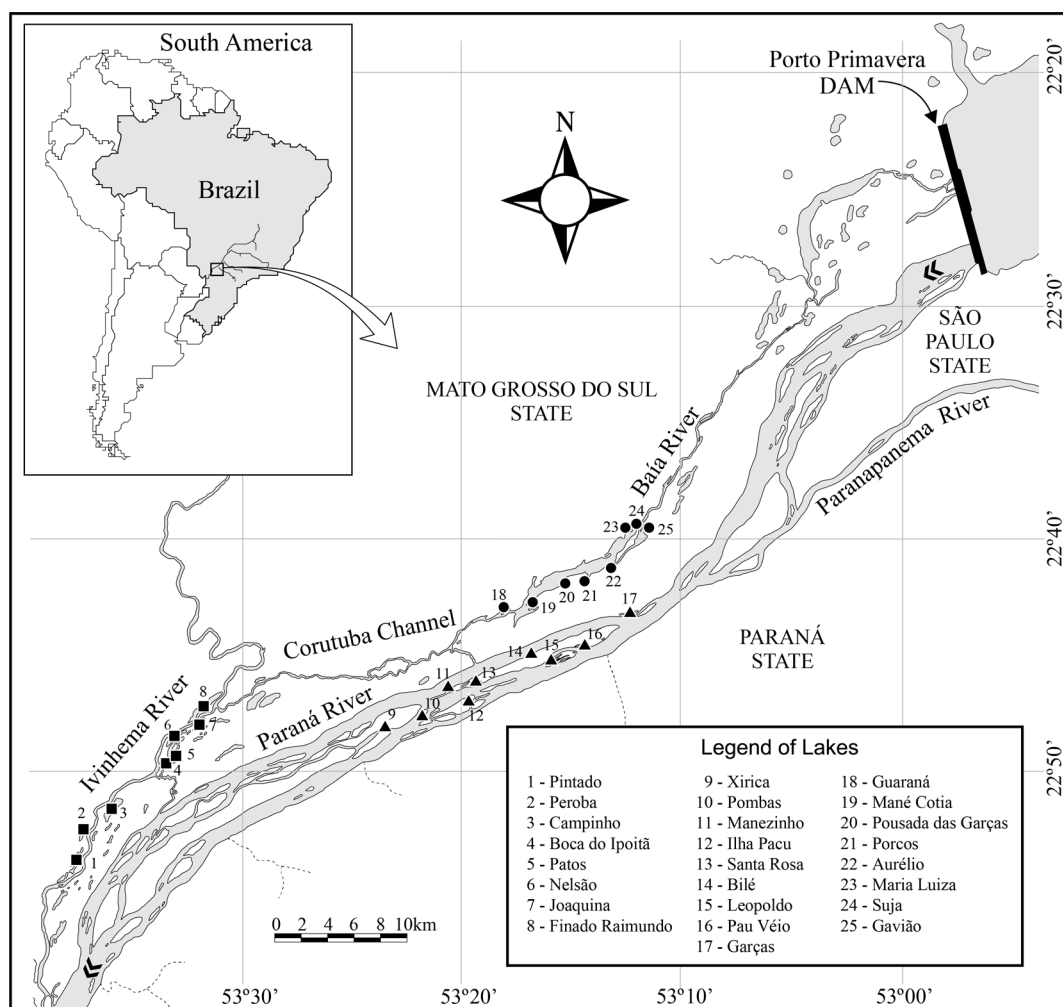

Fig. 1 Position of the twenty-five lakes in the Upper Paraná River floodplain, Brazil. Ivinhema (1–8), Paraná (9–17) and Baía (18–25) systems

Sampling and laboratory analysis

Ostracod communities associated with macrophytes were sampled between March 20th and 22nd in 2018. We collected samples of five life forms of macrophytes: emergent (EM), rooted floating (RF), free floating (FF), rooted submerged (RS) and free submerged (FS). The macrophytes species belonging to each life form, are shown in the Electronic Supplementary Material (Table S2), and they were classified according to their life form following Pott and Pott (2000).

To standardize our sampling effort, we collected one sample of each macrophyte life form in each lake (when present). The sampling sites of each lake (one for each macrophyte life form) were chosen visually, based on the largest macrophyte bed of each life form. This selection was made because the larger the patches, the higher the chance of a good representation of the ostracod community in terms of diversity (e.g., richness, density and composition). However, not all life forms of macrophytes were always found in all lakes (see Electronic Supplementary Material, Table S2). A total of 75 samples were collected in 25 lakes, with 20 RF samples, 19 FF samples, 17 EM samples, 10 FS samples and 9 RS samples.

Ostracods associated with emergent macrophytes were sampled with a rectangular hand net (28×14 cm and mesh size of 160 μm), which was moved amongst the plants. Macrophytes with RF, FF, RS and FS life forms were removed manually from the water and transferred to a plastic bucket (Campos et al. 2017). Either the entire plants or only the roots were washed to remove the ostracods. The material retained in the bucket was washed through a hand net (mesh size of 160 μm). The sampling methods have been shown as adequate to represent associated fauna (Higuti et al. 2009, 2010; Castillo-Escrivà et al. 2016b; Campos et al. 2017). All material was preserved in 70º ethanol buffered with sodium tetraborate. In the laboratory, ostracods were sorted using a stereoscopic microscope and were identified down to species level (Martens and Behen 1994 and articles included therein; Rossetti and Martens 1998; Higuti and Martens 2012a, 2012b, 2014; Higuti et al. 2013; Ferreira et al. 2020).

Ostracod traits and taxonomic information

Ostracods were classified according to the functional traits: locomotion mode, body size, presence/absence of spines, general body morphology and reproductive mode (Electronic Supplementary Material, Tables S3). The locomotion mode was differentiated, considering the presence/absence or the length of natatory setae on the Antenna, in two categories: swimmer (long setae) and non-swimmer (reduced setae or setae absent, Meisch 2000). The body size classification was based on the length (L) and height (H) of the ostracod carapace. These measurements were obtained mostly using scanning electron microscopy (SEM) and in some cases with a stereoscope microscope. The species were categorized as small ($L \leq 0.54$ mm and/or $H \leq 0.32$ mm), medium ($0.55 \leq L \leq 1.32$ mm and/or $0.33 \leq H \leq 0.72$ mm) and large ($L > 1.32$ mm and/or $H > 0.72$ mm) (Matsuda et al. 2015). Spines of any size were classified as present/absent, according to visual observations of the ostracod carapace in a stereoscope microscope and SEM. Amongst the species treated here, all spines (when present) were relatively large. Reproductive mode was differentiated in parthenogenic, sexual and mixed reproduction. Body morphology was distinguished in flat (laterally compressed) and rounded in dorsal or ventral view, according to Martens and Behen (1994) and articles included therein; Rossetti and Martens (1998); Meisch (2000); Higuti and Martens 2012a, b, 2014; Higuti et al. (2013) and Ferreira et al. (2020). All these traits were chosen owing to their importance in life history characteristics (e.g., body size, Matsuda el al. 2015), dispersal limitation (e.g., locomotion mode and body morphology, Matsuda et al. 2015), defence against predators (e.g. presence of spines) and population establishment (e.g., reproductive mode, Horne et al. 1998) of ostracod species. Besides, these are the traits for which we have complete information for all taxa found in our survey.

We used taxonomic distance based on the path lengths in the Linnean taxonomic trees as a proxy for phylogeny (Clarke and Warwick 1998; Winter et al. 2013). Six taxonomic levels were included in this taxonomic tree: species, genus, tribe, subfamily, family and superfamily, and we followed Meisch et al. (2019) for higher taxonomy (Electronic Supplementary Material, Table S4).

Environmental and spatial factors

Chemical and physical variables, such as pH and electrical conductivity (μS cm^{-1}) (YSI 63), dissolved oxygen (mg L^{-1}) and water temperature (ºC) (YSI 550A oximeter), and water transparency (black and white Secchi disk) were measured in situ. The perimeter (in km) of the lakes and length of the meandering channel that connect each lake to the main river (in km) were obtained through the Google Earth image program, all from images taken during the dry season. All these variables (see Electronic Supplementary Material, Table S1), were considered "environmental factors".

We generated the "spatial factors" calculating matrices of Euclidean distances ("overland", derived from geographical coordinates) of the sites. These matrices were submitted to the PCNM method (Principal Coordinates of Neighbour Matrices) for the construction of the eigenvectors (explanatory spatial variables, Borcard and Legendre 2002). The PCNM analysis was truncated by minimum distance that kept all sampling sites connected (minimum spanning tree

procedure, Landeiro et al. 2011). In the present study, the first PCNMs generated represent larger scales of amplitude, whereas the latter ones represent smaller scales of amplitude. Campos et al. (2019) compared three methods to generate spatial effects on ostracod metacommunities, "overland", "watercourse" (considering distances amongst the environments, following watercourse) and Asymmetric Eigenvectors Maps (AEM, considering the sampling sites connected in the watercourse, following the flow direction of the river), and showed that the results for "overland" were similar to the other methods.

Data analysis

We performed rarefaction curves to evaluate if the sampling effort for each macrophyte life form (20 RF samples, 19 FF samples, 17 EM samples, 10 FS samples and 9 RS samples) was sufficient to represent the associate ostracod communities in terms of richness over all 25 lakes. For that, we used Hill numbers through the function *iNEXT* (iNEXT R-package, Hsieh et al. 2016). The iNEXT R-package uses Chao 2 (for incidence data or "reference sample") to estimate the number of undetected species. We used $q = 0$ to estimate species richness and the maximum extrapolated size was up to 100% of the reference sample size. According to Heck et al. (1975), the occurrence of 50–75% of the estimated richness might be satisfactory (considering that most of the common species were recorded). We assessed possible differences in the ostracod composition amongst the life forms of macrophytes to highlight the relevance of analyzing each life form separately. For this, we first visualized the (dis)similarity in ostracod composition amongst the macrophytes life forms using the Principal Coordinate Analysis (PCoA, Legendre and Legendre 1998), based on a presence/absence matrix and Jaccard index. For testing such (dis)similarity, we performed a Multivariate Permutational Variance Analysis (PERMANOVA, Anderson 2006), using a total of 999 permutations. After that, we used a pairwise PERMANOVA to evaluate ostracod composition (dis)similarity amongst the macrophytes life forms. Finally, we performed Multivariate Dispersion Analysis (PERMDISP, Anderson 2006) to evaluate variability of the dispersion of ostracod communities amongst the macrophytes life forms. PERMDISP was based on a presence/absence matrix and Jaccard index, and the significance amongst the groups (macrophytes life forms) was tested using a total of 999 permutations. When PERMDISP results show significant differences in the variability of dispersal between groups, it can be related to differences in the scatter of data, indicating that the comparisons between groups (e.g., in PERMANOVA results) must be interpreted with caution. PERMANOVA and PERMDISP were performed using the vegan R-package (Oksanen et al. 2017).

We used distance-based redundancy analysis (db-RDA, Legendre and Anderson 1999), as well as variation partitioning procedures (Legendre et al. 2005) to evaluate the influence of environmental and spatial factors on ostracod beta-diversity facets, amongst different life forms of macrophytes. Before the analyses, we checked the multicollinearity amongst the environmental variables (environmental factors) using the variance inflation factor (VIF). Variables with VIF > 10 should be removed (Oksanen et al. 2017).

We used the function *beta* (BAT R-package, Cardoso et al. 2015) according to Perez Rocha et al. (2018) to generated three dissimilarity matrices (with Jaccard family measures): total beta-diversity (B-tot) and its components, replacement (B-repl) and richness difference (Rich-Diff), for each beta-diversity facet. These dissimilarity matrices were based on:

1) Species: sites x species matrices of presence-absence of ostracods;
2) Traits: we used the Gower distance (Gower 1971) to calculate between-species distances, based on the traits data, using the function *gowdis* (FD R-package, Laliberté et al. 2014). Subsequently, this species-by-species matrix was subjected to a hierarchical clustering (UPGMA agglomeration method) procedure using the function *hclust* (STATS R-package);
3) Phylogeny: we used ostracod taxonomic information as a proxy for phylogeny. We used the function *taxa2dist* (vegan R-package) to calculate taxonomic distance between ostracod species. Subsequently, this species-by-species matrix was also subjected to a hierarchical clustering (UPGMA agglomeration method) procedure using the function *hclust* (STATS R-package). The BAT R-package requires an *hclust* object to calculate beta-diversity metrics, thus clustering (phylogenetic tree, such as traits tree) was necessary (Perez Rocha et al. 2018).

After that, average beta-diversity (B-tot) and their components (B-repl and Rich-Diff), based on species, traits and phylogeny, were calculated using the function *beta.multi* (BAT R-package). This function returns three values (also named average values), which represent the total multi-site dissimilarity across the sites (B-tot) and its B-repl and Rich-Diff components. Finally, each of the dissimilarity matrices of each ostracod beta-diversity facet was used in the db-RDA and variation partitioning. The environmental and spatial factors, which should be included in the analyses, were selected using the function *ordiR2step* ($p < 0.05$, 999 permutations, vegan R-package). The db-RDA analyses were performed using the function *capscale* (vegan R-package). Subsequently, ostracod community variation in each of the beta-diversity measures (B-tot, B-repl and Rich-Diff) was

partitioned in purely environmental (E|S) and spatial factors (S|E), and in a component explained by the intersection of these factors (E ∩ S). The results were adjusted R^2 values and the significance of the components was tested using the *Anova* function ($p < 0.05$, vegan R-package). We used the *sqrt.dist* correction in all db-RDA analyses, for negative eigenvalues (Legendre 2014). All the analyses described above were performed separately for ostracod communities associated with each life form of macrophytes, using R 3.4 software (R Core Team 2017).

Results

Abiotic factors

The mean of the chemical and physical variables was more different between the Ivinhema and Paraná systems (Electronic Supplementary Material, Table S1). The Ivinhema system had the highest mean value of water temperature, lake perimeter and length of the meandering channel, while the Paraná system had the lowest values for the same variables. On the other hand, the Paraná system had the highest mean values of electrical conductivity, pH and water transparency, while the Ivinhema system had the lowest values for these variables. Mean values of all the variables in the Baía system were intermediate amongst the three systems. Lake perimeter, length of the meandering channel, dissolved oxygen and electrical conductivity were the variables that had the highest coefficient of variation amongst the lakes of all systems (see Electronic Supplementary Material, Table S1).

According to the spatial variables, 8 PCNMs were generated for EM, 9 PCNMs for RF, 6 PCNMs for FF and FS, and 4 PCNMs for RS. In EM, PCNMs 1–4 indicate broad-scaled and 5–8 fine-scaled patterns; in RF, PCNMs 1–5 indicate broad-scaled and 6–9 fine-scaled patterns; in FF and FS, PCNMs 1–3 indicate broad-scaled and 4–6 fine-scaled patterns; and in RS, PCNMs 1–2 indicate broad-scaled and 3–4 fine-scaled patterns.

Ostracod communities

We recorded 38 species of ostracods associated with 13 macrophyte species. Higher ostracod richness was found in RF (35 species), followed by FF (33), EM (30), RS (27) and FS (24) (Table 1). The observed richness represents between 82.17% (FS) and 98.45% (EM) of the estimated richness and the rarefaction curves show asymptotic levelling-off (Fig S1). These results suggest that the sampling effort was adequate to represent the ostracod communities in each macrophyte life form.

The PCoA and PERMANOVA results show significant differences in ostracod composition amongst the macrophyte life forms ($F = 2.02$; $p = 0.001$, Fig. S2). The pairwise PERMANOVA results show differences in the ostracod composition between free floating plants and all other macrophyte life forms (Table S5). The PERMDISP results show no significant differences in the variability of the dispersion of ostracod communities amongst the macrophytes life forms ($F = 0.64$, $P = 0.65$). The average distance from the centroid is similar amongst the macrophytes life forms: RS = 0.54, RF and FS = 0.52, EM = 0.51 and FF = 0.49. PERMDISP results thus show that differences in PERMANOVA results are not influenced by differences in the scatter of ostracod data amongst the macrophytes life forms (e.g., difference in the number of samples amongst macrophytes life forms), thus indicating that the data of these groups are comparable.

Average values of total beta-diversity and its components

In this section, we compare both differences amongst macrophytes life forms and amongst beta-diversity facets. The average values (derived from the dissimilarity matrices) of total species-based ostracod beta-diversity are higher than the traits- and phylogeny-based ones (Table 2). The total species-based beta-diversity (B-tot, average values ranging between 0.689 and 0.754) is mostly explained by B-repl in all macrophyte life forms (ranging between 55 and 67% of B-tot). Traits-based total beta-diversity (B-tot, average values ranging between 0.478 and 0.577) is more explained by B-repl in FF, EM and RS (60%, 57% and 54% of B-tot, respectively), and by Rich-Diff in FS and RF (55% and 52% of B-tot, respectively). Finally, phylogeny-based total beta-diversity (B-tot, average values ranging between 0.507 and 0.593) is more explained by B-repl in EM, RS, FF and RF (58%, 57%, 57% and 51% of B-tot, respectively), and by Rich-Diff in FS (61% of B-tot, Table 2).

Comparing factors affecting ostracod beta-diversity facets amongst macrophyte life forms

The influence of the environmental and spatial factors structuring ostracod beta-diversity facets are variable amongst different life forms of macrophytes (Fig. 2). The total percentage of explained variation (R^2) of the factors (sum of pure environmental, pure spatial and shared fraction) had the highest values in FS (up to 86%), followed by RF (up to 49%), FF (up to 44%), RS (up to 43%) and EM (up to 27%).

Variation partitioning shows that the environmental factors are important for ostracod beta-diversity facets in all macrophyte life forms, while higher percentages of explanation are found in submerged life forms (FS up to 68% and RS up to 32%), than in floating and emergent life forms (FF

Table 1 Ostracod species occurrence in different macrophyte life forms in the Upper Paraná River floodplain, indicating the number of lakes where each ostracod species was found, in each macrophyte life form

	EM (17)	RF (20)	FF (19)	RS (9)	FS (10)
Family Cyprididae (Baird 1845)					
Diaphanocypris meridana (Furtos 1936) Würdig and Pinto 1990	12	17	15	8	8
Stenocypris major (Baird 1859) Daday 1898	0	4	4	2	0
Stenocypris malayica Victor and Fernando 1981	0	3	3	3	1
Strandesia psittacea (Sars 1901) Roessler 1990	7	7	6	3	2
Strandesia colombiensis (Roessler 1990) Ferreira et al. 2020	5	6	4	1	3
Strandesia mutica (Sars 1901) G.W. Müller 1912	4	4	7	2	0
Strandesia variegata (Sars 1901) G.W. Müller 1912	3	2	6	0	2
Strandesia tolimensis Roessler 1990	1	5	8	0	1
Strandesia nakatanii Ferreira et al. 2020	6	5	0	3	2
Strandesia lansactohai Higuti and Martens 2013	5	2	0	3	0
Strandesia velhoi Higuti and Martens 2013	9	13	13	5	6
Strandesia nupelia Higuti and Martens 2013	4	4	3	0	0
Bradleytriebella trispinosa (Pinto and Purper 1965) Savatenalinton and Martens 2009	3	7	7	0	2
Bradleytriebella lineata (Victor and Fernando 1981) Savatenalinton and Martens 2009	0	0	1	0	1
Cypricercus alfredo Almeida et al. 2021	5	5	1	2	0
Chlamydotheca deformis Farkas 1958	12	15	15	7	6
Chlamydotheca iheringi (Sars 1901) Klie 1930	6	8	6	5	6
Chlamydotheca cf. *iheringi* sp. 2	7	11	7	2	2
Chlamydotheca sp. 3	3	5	3	1	0
Cypretta costata G.W. Müller 1898	0	2	0	0	1
Cypretta sp. 3 n.sp	8	11	16	2	2
Cypridopsis vidua (O.F. Müller 1776) Brady 1867	9	5	3	5	1
Cypridopsis cf. *vidua* sp. 2	3	1	0	3	1
"*Cypridopsis*" n. gen. 1 n.sp.	9	8	7	1	3
"*Cypridopsis*" n. gen. 2 n.sp.	0	1	2	0	0
Cabelodopsis hispida (Sars 1901) Higuti and Martens 2012b	0	1	4	0	0
Neocypridopsis nana (Sars 1901) Klie 1940	2	12	10	3	2
Family Candonidae (Kaufmann 1900)					
Candobrasilopsis brasiliensis (Sars 1901) Higuti and Martens 2012a	6	4	4	2	3
Candobrasilopsis rochai Higuti and Martens 2012a	7	5	3	1	0
Candobrasilopsis elongata Higuti and Martens 2014	5	2	7	0	1
Pseudocandona agostinhoi Higuti and Martens 2014	3	5	11	1	1
Pseudocandona cillisi Higuti and Martens 2014	3	0	5	0	0
Physocypria schubarti Farkas 1958	4	1	6	1	0
Candonidae n. gen. n.sp.	3	2	0	3	0
Family Limnocytheridae (Kile 1938)					
Cytheridella ilosvayi Daday 1905	16	17	15	6	9
Family Darwinulidae (Brady and Norman 1889)					
Alicenula serricaudata (Klie 1935) Rossetti and Martens 1998	3	6	13	2	1
Vestalenula pagliolii (Pinto and Kotzian 1961) Rossetti and Martens 1998	0	2	10	1	0
Penthesilenula brasiliensis (Pinto and Kotzian 1961) Rossetti and Martens 1998	0	0	5	0	0

EM emergent, *RF* rooted floating, *FF* free floating, *RS* rooted submerged and *FS* free submerged

Values in parenthesis indicate the number of lakes in which the macrophyte life forms were sampled

up to 19%, RF up to 13% and EM up to 19%). Spatial factors are mostly non-significant in structuring ostracod beta-diversity. However, significant percentages of explanation of these factors are found for B-repl in RF and FS (up to 30%), and for Rich-Diff in EM and FS (up to 21%). We do not observe higher percentages of explanation of spatial

Table 2 Average values of total beta-diversity (B-tot, total multi-site dissimilarity across the sites derived from the dissimilarity matrices) and its components (*B-repl* replacement and *Rich-Diff* richness difference), obtained through the function *beta.multi* in the BAT R-package

		Species					Traits					Phylogeny				
		Average values/%	E. sel	S. sel	P (E)	P (S)	Average values/%	E. sel	S. sel	P (E)	P (S)	Average values/%	E. sel	S. sel	P (E)	P (S)
EM	B-total	0.728	Ec	–	**0.001**	0.429	0.479	Ec	–	**0.001**	0.446	0.507	Ec	–	**0.001**	0.083
	B-repl	0.491 (67)	Ec	–	**0.001**	0.294	0.273 (57)	Ec	PCNM 6	**0.001**	**0.049**	0.296 (58)	Ec	PCNM1	**0.001**	**0.021**
	Rich-Diff	0.237 (33)	–	PCNM3	0.399	**0.05**	0.205 (43)	–	–	0.142	0.08	0.211 (42)	–	PCNM3	0.284	**0.032**
RF	B-total	0.724	Ec, Wt	–	**0.003**	0.848	0.506	pH	–	**0.012**	0.789	0.535	pH, Wt	–	**0.002**	0.292
	B-repl	0.487 (67)	pH, Len	–	**0.002**	0.313	0.243 (48)	pH	PCNM1, PCNM3, PCNM5, PCNM6	**0.005**	**0.001**	0.268 (51)	Ec	PCNM1, PCNM2, PCNM3, PCNM5, PCNM6	**0.046**	**0.002**
	Rich-Diff	0.237 (33)	–	–			0.263 (52)	Wt	–	**0.049**	0.21	0.266 (49)	Wt	–	**0.031**	0.408
FF	B-total	0.689	Ec, Do, Tr	–	**0.001**	0.376	0.478	Ec, Do, pH	–	**0.005**	0.184	0.512	Ec, Do, pH	PCNM2, PCNM5	**0.005**	**0.044**
	B-repl	0.459 (67)	Ec, Do, Tr	–	**0.005**	0.657	0.289 (60)	Ec, Do, Tr	PCNM1, PCNM2, PCNM5	**0.001**	**0.002**	0.292 (57)	Ec, Do	–	**0.001**	0.116
	Rich-Diff	0.23 (33)	–	–			0.189 (40)	–	–			0.219 (43)	–	–	0.312	0.416
RS	B-total	0.754	–	–	0.891	0.899	0.577	Ec, Do	–	**0.05**	0.358	0.593	–	–	0.09	0.11
	B-repl	0.477 (63)	–	–	0.237	0.786	0.31 (54)	Ec, Do	–	**0.012**	0.606	0.339 (57)	pH, Wt	–	**0.028**	0.162
	Rich-Diff	0.276 (37)	–	–	0.814	0.672	0.266 (46)	–	–	0.336	0.325	0.254 (43)	–	–	0.079	0.908
FS	B-total	0.733	Ec, pH	–	**0.002**	0.234	0.519	Ec, pH	–	**0.002**	**0.039**	0.524	Ec	PCNM1	**0.042**	**0.049**
	B-repl	0.406 (55)	Ec, pH, Tr	PCNM5	**0.001**	**0.026**	0.231 (45)	Ec, pH	–	**0.001**	0.456	0.203 (39)	Ec	PCNM5	**0.002**	**0.026**
	Rich-Diff	0.327 (45)	–	PCNM1	0.538	**0.001**	0.288 (55)	–	PCNM1	0.485	**0.021**	0.32 (61)	–	PCNM1	0.498	**0.039**

Values in parenthesis indicate the percentage that the B-repl or Rich-diff represent of the B-tot. Environmental (*E. sel.* environmental variables selected) and spatial (S. sel. = PCNMs selected) variables selected for the pRDA, and *P* significance of this factors (P (E) and P (S)) for each beta diversity facet, in different macrophyte life forms. *EM* emergent, *RF* rooted floating, *FF* free floating, *RS* rooted submerged and *FS* free submerged. *Ec* electrical conductivity, *Tr* water transparency, *Wt* water temperature, *Do* dissolved oxygen, *Per* lake perimeter and *Len* length of the meandering connecting channel. Values in bold were significant at *P* < 0.05. In EM, PCNMs 1–4 indicate broad-scaled and 5–8 fine-scaled patterns. In RF, PCNMs 1–5 indicate broad-scaled and 6–9 fine-scaled patterns. In FF and FS, PCNMs 1–3 indicate broad-scaled and 4–6 fine-scaled patterns. In RS, PCNMs 1–2 indicate broad-scaled and 3–4 fine-scaled patterns
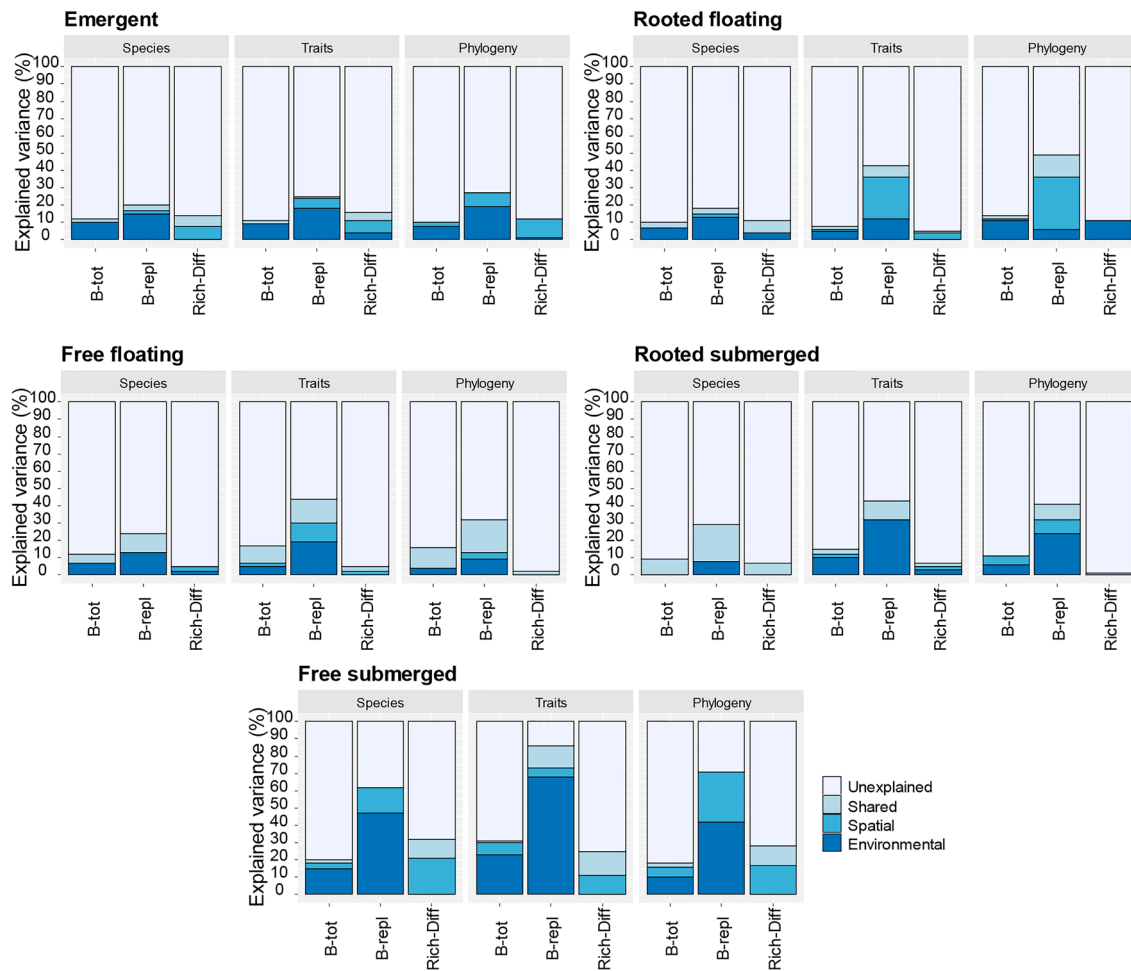
Fig. 2 Results of variation partitioning analyses showing the relative contributions (% of explanation) of the environmental, spatial, shared fraction between environmental and spatial factors and the unexplained fraction for each beta diversity measure (*B-tot* beta total, *B-repl* replacement and *Rich-Diff* richness difference), amongst the facets of ostracod beta diversity, in different macrophyte life forms

factors in rooted life forms (EM, RF and RS), as compared to the free-living ones (FF and FS, Fig. 2). Shared fractions between environmental and spatial factors are high (up to 21%, Fig. 2) in some life forms, mainly in FF and RS.

Factors affecting each facet of ostracod beta-diversity

In general, the influence of the environmental factors is high for B-repl (up to 68%) and low for B-tot (< 24%) and Rich-Diff (< 12%) for all beta-diversity facets. However, this influence is variable amongst the beta-diversity facets. Frequently, the percentages of explanation of environmental factors are higher for B-tot (ranging between 5 and 23%) and B-repl (ranging between 12 and 68%) for traits-based beta-diversity, than for those of species- (B-tot ranging between 0 and 15%, B-repl ranging between 8 and 47%) and phylogeny-based beta-diversity (B-tot ranging between 4 and 11%, B-repl ranging between 6 and 42%). As environmental factors were always less explanatory for Rich-Diff, we do not see differences in their influence amongst the beta-diversity facets. The percentages of explanation of spatial factors are always low (< 31%) for all beta-diversity facets. Higher values for such effects of spatial factors are observed for B-repl (up to 30%) as compared to Rich-Diff (up to 21%) and B-tot (up to 7%). The influence of spatial factors is higher for phylogeny-based beta-diversity (up to 30%) than for species- (up to 21%) and traits-based beta-diversity (up to 24%, Fig. 2).

Selected environmental and spatial factors

In this section, we compare selected environmental and spatial variables in the db-RDA models, both amongst macrophytes life forms and amongst ostracod beta-diversity facets. Considering the environmental factors, the selected variables are quite similar amongst the beta-diversity facets

but quite different amongst the macrophytes life forms (Table 2). Furthermore, the environmental variables are frequently significant for B-tot and for B-repl components, but are rarely significant for the Rich-Diff component, for all beta-diversity facets in all macrophytes life forms. The most frequently selected environmental variables are electrical conductivity (e.g. for B-repl of all beta-diversity facets in almost all macrophytes life forms), pH (e.g., for B-repl of species- and traits-based beta-diversity in FS and FF; and for B-tot of trait- and phylogeny-based beta-diversity in RF, FF and FS), dissolved oxygen (e.g., for B-tot and B-repl of all beta-diversity facets in FF), and water temperature (e.g., for B-tot of species- and phylogeny-based beta-diversity in RF, Table 2). Considering the spatial factors, the generated PCNMs are rarely selected for species-based beta-diversity in all macrophytes life forms (Table 2). For traits-based beta diversity, the selected PCNMs are variable amongst macrophytes life, representing fine-scaled (e.g. PCNM6 for B-repl in EM) broad-scaled (e.g., PCNM1 for Rich-Diff in FS), and both fine- and broad-scaled spatial patterns (e.g. PCNM1, PCNM3, PCNM5 and PCNM6 for B-repl in RF). Similarly, for phylogeny-based beta-diversity, the selected PCNMs represent fine-scaled (e.g., PCNM5 for B-repl in FS), broad-scaled and both fine- (e.g., PCNM1 for Rich-Diff and PCNM3 for B-tot in EM) and broad-scaled spatial patterns (e.g. PCNM1, PCNM2, PCNM3, PCNM5 and PCNM6 for B-repl in RF, Table 2).

Discussion

Environmental and spatial effects amongst different macrophyte life forms

Environmental factors significantly structure ostracod beta-diversity facets and their percentages of explanation were higher for submerged macrophytes life forms, compared to the floating and emergent ones, supporting the first hypothesis of the present study. This pattern of percentage of explanation of the environmental factors may reflect the presence and repartition of the life forms in the water column, which are important factors in determining habitat structure (Choi et al. 2014). Such occupancy creates a higher variation in chemical and physical characteristics of the water around the roots (or even around the entire plant). For example, submerged macrophytes can live in a great variety of depths, compared to floating macrophytes, because they are adapted to regions where transparency is higher (Meerhoff et al. 2003), apart from the fact that they themselves also have the capacity to increase the water clarity by reducing nutrients (Scheffer et al. 1993). On the other hand, floating macrophytes (FF or RF) penetrate less in the vertical dimension as compared to the EM ones, and might furthermore reduce

the light penetration in the water column owing to the floating leaves that form patches on the water surface (Cattaneo et al. 1998; Cremona et al. 2008). Floating macrophytes can still supply oxygen to the water around the roots, as they can transport oxygen from the atmosphere to these structures (Rehman et al. 2017). Consequently, ostracod species (or sets of traits and phylogenetic lineages of ostracods) may have been sorted, mainly in submerged life forms, owing to their physiological tolerances to certain environmental conditions. For example, some ostracod species are very sensitive to low concentrations of dissolved oxygen, as shown by Ruiz et al. (2013), and we observe lower concentrations of this variable around submerged macrophytes (see also below in "Selected environmental and spatial factors").

In addition, we find that environmental factors had a higher influence on ostracod beta-diversity facets in FS macrophytes than in other life forms. The FS life form was represented by *Utricularia foliosa*, which is known as a "carnivorous plant". This plant genus is adapted to life in aquatic regions that are poor in nutrients, and they remove these directly from the water or from their prey (Adamec 2008). Guisande et al. (2000) showed that there is a relationship between the decrease of zooplankton abundance and the increase in the number of bladders (for prey) per leaf in *U. foliosa*, as an adaptation to improve its carnivory and input of nutrient. These authors also showed that higher electrical conductivity had a negative influence on the bladder production of *U. foliosa*. Although we did not measure bladder productivity of *U. foliosa* in the present study, we infer that electrical conductivity may have indirectly influenced ostracod communities by increasing (or decreasing) the quantity of these plant structures. For example, some species of ostracods may have been more easily trapped by plants with higher numbers of bladders, which have led to such higher environmental influence on beta-diversity facets in our survey.

Spatial factors have some importance in structuring ostracod beta-diversity facets and we did not find higher values of spatial effects on ostracods associated with fixed macrophyte life forms, indicating that ostracods might present some dispersal limitation, regardless of the plant dispersal capacity, thus refuting our second hypothesis. Despite the fact that ostracods in general are good passive dispersers, especially the species of the family Cyprididae (Meisch 2000; Brochet et al. 2010; Pereira et al. 2017), several studies have also found spatial effects on ostracod communities, related to dispersal limitation (Castillo-Escrivà et al. 2016a, 2017; Campos et al. 2019).

We highlight that the environmental and spatial factors discussed here explain at most 25% of the variability in ostracod beta-diversity in some macrophyte life forms (e.g., EM) in the Upper Paraná River floodplain. A high shared fraction of environmental and spatial factors in some cases

(e.g., 21% in species-based beta-diversity in RS), suggests that part of the environmental gradient was spatially structured, which may, for example, have led to a decrease in the effect of environmental or spatial factors.

Differences amongst the beta-diversity facets and their components

Our results show that there were mismatches in the factors structuring each of the ostracod beta-diversity facets in each of the macrophyte life forms. This is so, because communities consist not only of different taxonomic assemblages but also of species with different traits (Alahuhta et al. 2019). Thus, using different data (either species-, traits- or phylogeny-based) on beta-diversity metrics can show species responding differently to the environmental gradient (e.g., variation in habitat formed by the different macrophyte life forms), thus generating a mismatch in the factors affecting each beta-diversity facet (Devictor et al. 2010). Similarly, Cai et al. (2019) found that the effect of the factors structuring the beta-diversity of freshwater molluscs, such as geography, energy and environment, were different amongst the three facets. However, such pattern of mismatches in the factors affecting the beta-diversity facets depends on the biological group under study. For example, Perez Rocha et al. (2018) found that local environment and space were factors that affected all the facets of macroinvertebrates beta-diversity in streams of western Finland in a similar way.

Considering the total beta-diversity, our results indicate that high species-based beta-diversity does not necessarily indicate high traits- and phylogeny-based beta-diversity. This might be related to the redundancy in the set of traits of ostracod species amongst the lakes, or even to the lack of information about other (unknown) ostracod traits (such as feeding preferences, behavioral responses to light or predators, parasites and burrowing abilities), which might have led to a lower traits-based diversity. Braghin et al. (2018), analysing zooplankton communities in the lakes of the Paraná River, also found lower functional beta-diversity, because species that were replaced amongst the environments probably had functional redundancy. Likewise, the set of ostracod species amongst the environments may have closely related taxonomic levels (same genus, same subfamily, …), which led to a lower phylogeny-based beta-diversity. According to Graham and Fine (2008), if lineages have conserved phylogenetic niches, species might be expected to be sorted by habitat, whereas if their phylogenetic niche is variable, closely related species are predicted to exist in different habitats. Our results indicated that (phylogenetically) closely related ostracod species might present conserved phylogenetic niches.

The fact that the replacement component was the main driver of the ostracod beta-diversity facets, in almost all

macrophyte life forms, confirms that the variation in the environmental conditions replaces species (or traits and lineages of ostracod) from one lake to another. This might be associated with the difference in ecological conditions throughout the systems of the Paraná River floodplain (such as electrical conductivity which was the most variable amongst the systems). For example, the Paraná system can present lower environmental heterogeneity than the Ivinhema and Baía systems (Higuti et al. 2009), because of the effects resulting from dam regulation (Braghin et al. 2018), which evens-out or even eliminates small water level changes that are still present in the other two rivers.

Selected environmental and spatial factors

Most studies evaluating the influence of environmental factors on ostracod community structure are species-based, and this information is less applicable using the other facets of ostracod beta-diversity. Only one previous study (Marmonier et al. 1994) showed that environmental variables (such as variation of habitat characteristics) had an effect on traits-based diversity of ostracods, and the distribution of the set of traits of this community was found to be related to the habitat type. The selected variables in the present study, such as dissolved oxygen, electrical conductivity, pH and water temperature, are known to be important for the structure of ostracod communities in species-based studies. For example, such studies have found a correlation between ostracod community attributes and dissolved oxygen (Nagorskaya and Keyser 2005; Higuti et al. 2017) and electrical conductivity (Liberto et al. 2012). pH was relatively acidic in some lakes of the Upper Paraná River (Table S1), and this parameter was probably selected because low values of pH might affect freshwater ostracod valve calcification. Most ostracod species prefer alkaline or only slightly acidic waters (Ruiz et al. 2013; Mesquita-Joanes et al. 2012 and references therein). Finally, water temperature can affect the (length of the) life history and resulting body size of the adult organisms, i.e. the development rate of species might accelerate with increasing temperature (Aguilar-Alberola and Mesquita-Joanes 2014; Castillo-Escrivà et al. 2016a).

The spatial factors selected here indicate that dispersal limitation might have influenced some ostracod beta-diversity facets (and their components), from narrow (e.g., within systems of the Paraná River floodplain) to broad (e.g., amongst systems) scales of variation, differently in the different macrophyte life forms.

Conclusion

Environmental factors are significantly structuring ostracod beta-diversity facets, mainly for submerged macrophytes. This is probably related to the variation in water

chemical and physical characteristics around the roots (or entire body) of these life forms, which replaces species (or ostracod traits and lineages), according to their ecological niche, thus affecting beta-diversity patterns. Furthermore, environmental and spatial factors have different influence on each of the beta-diversity facets, thus highlighting the importance to include these three approaches (species-, traits- and phylogeny-based) in ecological surveys. Therefore, biological communities associated with different macrophyte life forms should be considered in local as well as regional biodiversity surveys, owing to the variation in the factors affecting these communities associated with each macrophyte life form. In addition, we stress the importance of preservation and management of the different macrophyte life forms in river-floodplain ecosystems, as they provide higher diversity of available habitat for associated biological communities. Besides, we predict that if more dams are constructed (e.g., in Paraná River and its adjacent tributaries) and the diversity of macrophyte life forms is negatively affected, direct effects might change the structure of associated communities such as invertebrates and small fish.

Compliance with ethical standards

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