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# Multi-scale analysis of functional plankton diversity in floodplain wetlands: Effects of river regulation



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#### HIGHLIGHTS

#### GRAPHICAL ABSTRACT

- River regulation alters hydrological dynamics and threatens floodplain biodiversity.
- Plankton diversity was analysed in wetlands in free-flowing and impounded stretches.
- Wetlands in the free-flowing stretch hosted lower alpha and higher beta diversity.
- Some ecological traits were nearly absent in the wetland of the impounded stretch.
- The gradient of hydrological connectivity is a main driver of plankton diversity.

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# ABSTRACT

Riverine floodplains are among the most diverse and dynamic ecosystems, but river regulation measures have altered the natural hydrological regime threatening their ecological integrity. We compared spatial patterns of phyto- and zooplankton functional diversity and of environmental heterogeneity between floodplain wetlands located in free-flowing and impounded stretches of the Danube River (Austria). We included two nested spatial scales (different habitats and water sections within wetland areas) and two contrasting hydrological conditions (post-flood, no flood). Environmental heterogeneity was lower in the wetland in the impounded stretch than in the free-flowing ones. At post-flood conditions, increased alpha diversity of rotifers and microcrustaceans and decreased beta diversity of phytoplankton and rotifers occurred in the impounded stretch as compared to the wetlands in free-flowing one. Beta diversity was higher between water sections than between habitats in freeflowing wetlands and similar across scales in the wetland in the impounded stretch. Regarding functional composition, the wetland in the impounded stretch hosted more homogeneous communities, as some ecological traits were nearly absent. Our results indicate that patterns of functional diversity in floodplain wetlands affected by river regulation are altered, highlighting the major role of the gradient of lateral connectivity and dynamic water level fluctuations as drivers for planktic diversity in river floodplains. This study contributes with essential knowledge to optimize restoration and diversity conservation measures in riverine ecosystems. © 2019 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (http://

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# 1. Introduction

Analysing and understanding patterns of biodiversity distribution are fundamental interests in ecology. The unprecedented high rates of anthropogenic transformations of the biosphere raise the important question of their impact on biodiversity, especially in riverine systems (Vörösmary et al., 2010). The regional diversity ( $\gamma$ -diversity) can be split into the local diversity ( $\alpha$ -diversity) and the variation in species composition among localities (β-diversity) (Whittaker, 1972). According to the niche theory (Hutchinson, 1957), the spatial variation of species distribution is a consequence of their responses to environmental gradients, based on the assumption that species differ depending on their ecological traits. It is hypothesized that more heterogeneous habitats offer more niches and possibilities to exploit resources, thus promoting enhanced  $\beta$  and  $\gamma$  diversities (MacArthur and MacArthur, 1961; Whittaker, 1972). In this context, environmental heterogeneity and ecological differences among species are key aspects to understand biodiversity patterns. A large body of research has addressed the relationship between biodiversity and environmental heterogeneity along a broad range of scales, though most of these studies have focused on species identity (i.e. taxonomic diversity) ignoring the variety of ecological traits (i.e. functional diversity) (Levin, 1992; Declerck et al., 2011; Heino et al., 2013; Chaparro et al., 2015). Ecological traits are morpho-physiophenological attributes that impact organism's fitness through their effects on growth, reproduction and survival (Violle et al., 2007). Trait-derived diversity indexes summarise the values and ranges of traits represented in communities, thus providing a more mechanistic understanding of their responses to environmental gradients (Gianuca et al., 2018; Abonyi et al., 2018; Braghin et al., 2018; Rumm et al., 2018).

Natural riverine floodplains are among the most important biodiversity hosts of the world, and this is mainly attributed to their elevated temporal variability and spatial heterogeneity at multiple scales (Junk et al., 1989; Tockner and Stanford, 2002). Aquatic environments present different extents of hydrological connectivity with the main channel, depending mainly on the flow pattern and their distance and height position relative to the river channel (Hillman and Quinn, 2002). This produces highly heterogeneous water bodies at the floodplain scale, ranging from lotic, turbid, nutrient-rich and frequently disturbed to lentic, clear and vegetated conditions (Amoros and Bornette, 2002; Schiemer et al., 2006; Keruzoré et al., 2013). At a smaller scale, patches of macrophytes with distinct life forms contribute to a large environmental heterogeneity within water bodies (Boschilia et al., 2008; Thomaz et al., 2007) and provide habitats for zooplankton and other organisms (Thomaz and Cunha, 2010).

Consequently, phyto- and zooplankton comprise a huge diversity of ecological strategies that vary along floodplain environmental gradients: from small fast-growing phytoplankton taxa adapted to turbulent waters to large slow-growing organisms adapted to more stable conditions (Devercelli et al., 2014; Schagerl et al., 2009; Baranyi et al., 2002), and from pelagic filter feeding to scraping zooplankton taxa associated with macrophytes (Van den Brink et al., 1994; Chaparro et al., 2015).

Spatial patterns of phyto and zooplankton diversity were mainly addressed with a taxonomic approach, observing a relationship with environmental conditions driven by the discharge regime of the river. Periods of high waters can either result in abiotic homogenisation and decreased  $\beta$ -diversity, as consequence of higher connectivity between the aquatic habitats (Thomaz et al., 2007; Bozelli et al., 2015), or in enhanced  $\beta$ -diversity resulting from flood-driven environmental gradients (Nabout et al., 2007; Simões et al., 2013). Phytoplankton and rotifers alpha diversity increases at high or intermediate water levels (Riedler et al., 2006; Borges and Pedrozo, 2009; Chaparro et al., 2015) and microcrustaceans show the opposite pattern (Baranyi et al., 2002). Studies addressing plankton diversity across scales revealed that  $\beta$ -diversity associated to the gradient of hydrological connectivity is a major component of  $\gamma$ - diversity in dynamic floodplain systems (Simões et al., 2013; Moresco et al., 2017; Dittrich et al., 2016; Chaparro et al., 2018).

Due to dramatic rates of river intervention worldwide (Agostinho et al., 2004; Zarfl et al., 2014), dams and artificial levees have blocked the dynamic effect of the flood regime in most floodplain areas in large rivers. Though evidence supports the fundamental role of dynamic water levels on diversity distribution in floodplains, little is known about the effects that river regulation might exert on such patterns. Among the expected consequences, the decrease of the essential environmental heterogeneity for the maintenance of biological diversity is a major threat (Ward et al., 2002). Considering that organisms's response to environmental changes are mediated by their ecological traits (Litchman et al., 2013), more homogeneous floodplain habitats are expected to host communities with decreased functional diversity (Braghin et al., 2018; Oliveira et al., 2018). The use of a functional approach will improve our knowledge of mechanisms driving diversity distribution and of its effects on ecosystem functioning (Mason and de Bello, 2013), and hence allow planning adequate mitigation and restoration measures.

We compared phytoplankton, rotifer and microcrustacean zooplankton (copepods and cladocerans) functional diversity ( $\alpha$ ,  $\beta$ ,  $\gamma$ ) and composition between floodplain wetlands located in free-flowing (FF) and impounded (IM) stretches of the Danube River in Austria. Besides differing in their flow conditions, there is a gradient of hydrological connectivity of the water sections in FF wetlands, which is absent in the IM wetland. We included two nested spatial scales: (i) *habitats* determined by the absence-presence of different macrophyte life forms, and (ii) *water sections* within floodplain wetlands, and two contrasting hydrological conditions (post-flood, no flood).

We tested the following hypotheses: 1- homogeneous conditions related to low and continuous hydrological connectivity favour a limited number of ecological traits in the communities and thus determine decreased  $\alpha$ - functional diversity in the impounded stretch, as compared to the FF wetlands; 2- the gradient of hydrological connectivity in wetlands in the free-flowing stretch promotes high environmental heterogeneity, favouring communities with a high variety of ecological traits and thus enhancing  $\beta$ - and  $\gamma$ -diversities; 3- in wetlands from the freeflowing stretch, environmental heterogeneity and  $\beta$ -diversity are higher *between sections* (where the gradient of hydrological connectivity occurs) than *between habitats*, and these are similar across scales in wetlands from the impounded stretch.

## 2. Materials and methods

#### 2.1. Study area

The Danube River is 2900 km long and drains an area of 817,000 km<sup>2</sup>; at Vienna (Austria), its mean annual discharge is about 1950 m<sup>3</sup> s<sup>-1</sup>. Regulation measures beginning mainly in 1875 constrained a vast floodplain area. To recover the hydrological connectivity, a large-scale restoration program was performed along the freeflowing stretch of the Danube downstream of Vienna (Fig. 1a). In two wetlands, Regelsbrunn and Orth, abandoned side channels were reconnected to the Danube River by reactivation of former inflow channels, removal of check dams and creation of additional outlets (Tockner and Schiemer, 1997; Schiemer et al., 1999). Today there is a broad range of hydrological connectivity between the main channel and floodplain waterbodies, and the area is among the last remnants of riverfloodplain systems in mid Europe (Schiemer et al., 1999; Reckendorfer et al., 2006). In Lobau, a wetland system within city limits of Vienna, the restoration included only one levee opening at its lowermost end (Schiemer et al., 1999); despite recovering a dynamic hydrology, this floodplain area has a limited connection to the main channel. The free-flowing section that comprises the three dynamic wetlands was given the status of a national park in 1996 (Donau-Auen National Park, DANP, Fig. 1b). Greifenstein is a floodplain wetland located in an



Fig. 1. a. Map with the geographic location of the floodplain areas along the Danube River in Austria: Greifenstein (IM1) in an impounded stretch and DANP (Donau Auen National Park) in a free-flowing (FF) one; b. detail of the of the water sections from the wetlands in the DANP: Orth (FF1), Regelsbrunn (FF2), and Lobau (FF3) and c. from the Greifeinstein (IM1) wetland.

impounded stretch of the Danube River, between the Altenworth and Greifenstein hydropower stations upstream Vienna (Fig. 1c). Here, weirs control the connectivity of the aquatic environments to the main channel independently from the water level fluctuations of the river, thus determining rather constant and intermediate connectivity conditions in all water sections (Edinger, 2009). The three dynamic wetlands within the free-flowing stretch, Orth (FF1), Regelsbrunn (FF2) and Lobau (FF3) and the more hydrologically stable Greifenstein wetland in the impounded stretch (IM1) were compared in this study.

#### 2.2. Field sampling

Phyto and zooplankton communities were sampled at two nested spatial scales in each wetland: 1- water sections which, in the freeflowing section were located along a gradient of hydrological connectivity with the main channel ranging from 0 to 365 days year  $^{-1}$ (Reckendorfer et al., 2006) and, in the impounded stretch had the same average connectivity level, 23 days year <sup>-1</sup> (Edinger, 2009); 2habitats (open waters, submerged macrophytes, floating-leaved macrophytes and helophytes) within each water section whenever present. To avoid possible effects associated to variations in vegetation cover, the selected vegetated patches had near 100% of plant cover. To compare contrasting hydrological conditions associated to the river discharge regime, the sampling was performed two times in each site: once in summer 2014 within 3 to 10 days after a flood pulse that inundated most of the wetland areas in the free-flowing section (post-flood) and once in summer 2015, during a low flow period with no flood event (no flood). In total, 46 and 35 sampling sites were included at post-flood and no flood conditions, respectively.

#### 2.3. Phyto and zooplankton species abundance

Samples for phytoplankton were taken at each sampling site, preserved with 1% Lugol's iodine solution, identified to the lowest possible taxonomic level (mostly species) using specialized literature and enumerated following Utermöhl (1958) with a counting error below 20%. Samples for zooplankton were collected at each sampling site with a transparent acrylic bottle (12 cm diameter) adequate for shallow open and vegetated waters (Paggi et al., 2001). Twenty liters of water from each site were filtered through a 40-µm mesh sieve and preserved with 4% formaldehyde. Rotifers, adult copepods and cladocerans were identified to the lowest possible taxonomic level (mostly species) using specialized literature under optical microscope. Rotifers were counted in a 1-mL Sedgwick-Rafter counting cell using an optical microscope; subsamples were taken with a Hensen-Stempel pipette. Adult copepods and cladocerans were examined and enumerated in a 5-mL Bogorov chamber under a stereomicroscope and subsampled with a Russell device. The counting error was below 10%.

# 2.4. Species ecological traits

The ecological characterization of phyto- and zooplankton was done for those species registered at least two times in our study (frequency of occurrence >1; i.e., 203 phytoplankton species, 89 rotifers, 26 cladocerans and 9 copepod species— Suppl. material S1). Phytoplankton was characterized by 11 ecological traits: mean biovolume, greater axial dimension, life form, nitrogen fixation ability, silica requirement, mixotrophy ability, pigment composition, presence of mucilage, akinete production, presence of flagella, presence of aerotopes. All zooplankton species were characterized by the mean body length and habitat preference; additionally, rotifers were characterized by the body type, trophi type and feeding mode; cladocerans by the filtration type, diet and feeding mode, and copepods by the diet. More detailed information on selected traits and literature consulted is provided in the Suppl. material S2.

#### 2.5. Environmental variables

Water temperature, pH, conductivity and dissolved oxygen (the latter only for the post-flood sampling) were measured in situ in each sampling site using HQd Hach® portable meter, water depth with a wooden meter and flow velocity with a Flo-Mate 2000 (Marsh-Mc Birney). Water samples were collected and immediately filtered using pre-combusted GF/F (Whatman) fiberglass filters for dissolved nutrients, total dissolved organic carbon (DOC) and suspended solids (SS) analyses. Soluble reactive phosphorus, ammonium and nitrate were measured using a continuous flow analyzer (CFA, Systea Analytical Technology). An aliquot of 30 ml filtered sample was acidified 3% v/vusing 2 M HCl and DOC was analysed using a Sievers 900 Portable TOC Analyzer (GE Analytical Instruments). The SS were determined drying the non-filterable residue at 103-105 °C until constant weight (American Public Health Association, 2005). Samples for chlorophyll-a were filtered through Whatman GF/C filters and stored at -20 °C for 24 h, homogenized with a Polytron-mixer (PT 1600E) and extracted with 5 ml cold 90% acetone overnight. After centrifugation (2500 rpm, 20 min), chlorophyll-a content was determined spectrophotometrically (Lorenzen, 1967; Jeffrey and Humphrey, 1975).

## 2.6. Data analyses

The environmental variables water depth, concentration of suspended solids, DOC, phosphate, nitrate and ammonium for both hydrological conditions were cube root transformed to normalise their distribution. Environmental heterogeneity was calculated with Euclidean distance based on standardized data (with the "range" method of the function decostand from the R package vegan); comparisons among wetlands were performed separately for each hydrological condition through a permutational test of multivariate homogeneity of groups dispersions. Pairwise comparisons were made by Tukey tests. Additionally, the environmental heterogeneity *between water sections* and *between habitats* was calculated and plotted for each wetland to explore changes across spatial scales for each hydrological condition.

All components ( $\alpha$ ,  $\beta$  and  $\gamma$ ) of functional diversity were calculated separately for each group (phytoplankton, rotifers and microcrustaceans), wetland and hydrological condition. The functional  $\alpha$ -diversity was assessed with number of unique traits combinations (UTC, Laliberté and Legendre, 2010) and the Rao's quadratic entropy Q (Rao's Q), which represents the mean distance between two randomly selected individuals. Functional diversity parameters were derived from the dbFD function in the FD package (Laliberté and Legendre, 2010) in R. Measures of diversity were tested for differences between wetland areas with one-way ANOVA. Homocedasticity was checked with the Levene Test. Tukey tests were used for post-hoc comparisons. The Community Weighted Mean trait value (CWM), which represents the dominant traits in a community (Ricotta and Moretti, 2011), was calculated for each site with the dbFD function. Then, functional  $\beta$ -diversity was assessed as the Gower distance calculated on CWM. Comparisons of functional  $\beta$ -diversity among wetlands were performed through a permutational test of multivariate homogeneity of group dispersions. Pairwise comparisons of group mean dispersions were made by Tukey tests. Functional  $\beta$ -diversity *between water sections* and *between habitats* were calculated and compared in each wetland. The functional  $\gamma$ -diversity with the parameters used for functional  $\alpha$ -diversity but on pooled data by wetland.

To assess community composition in the studied wetlands, Principal Component Analysis (PCA) based on CWM matrices were performed separately for each group and hydrological condition.

#### 3. Results

#### 3.1. Environmental heterogeneity

Environmental heterogeneity differed between wetlands, being overall lower in IM1, higher in FF1 and FF2, and intermediate in FF3 (Fig. 2). The wetlands from the free-flowing stretch (FF1, FF2 and FF3), showed a broader range of variation of habitat environmental conditions than the impounded wetland (Table S1). All the sites located in the impounded stretch presented similar and higher NO<sub>3</sub> concentrations (>120 µg l<sup>-1</sup>) and lower water temperatures (<18.6 °C) than those in the free-flowing stretches. Accordingly, in the impounded wetland PO<sub>4</sub> concentrations always exceeded 8.7 µg l<sup>-1</sup> during post-flood conditions.

# 3.2. Plankton functional diversity across spatial scales

Phytoplankton functional  $\alpha$ -diversity (UTC) was similar among all wetlands in both hydrological conditions (Fig. 3). Nevertheless, the alpha diversity range within each wetland was usually much lower in IM1. For rotifers, the functional  $\alpha$ -diversity was higher in IM1 and FF2 for post-flood and similar among wetlands for no flood, when only FF3 differed from IM1 (Fig. 3). For microcrustaceans, the functional  $\alpha$ -diversity was higher in IM1 and FF3 for post-flood and similar among all wetlands for no flood condition (Fig. 3). In general, the Rao's Q index followed very similar patterns to those of UTC (data not shown).

Phytoplankton functional  $\beta$ -diversity was higher in the three wetlands from the free-flowing stretch than in the impounded one at post-flood conditions, and similar between all wetlands at no flood (Fig. 4). Rotifer post-flood functional  $\beta$ -diversity was higher in FF1 and FF2 than in FF3 and IM1 for post-flood, with similar values among wetlands in no flood conditions (Fig. 4). Microcrustacean functional  $\beta$ diversity was similar among all wetlands in both hydrological conditions (except for lower values in FF2 in no flood).



Fig. 2. Environmental heterogeneity measured in wetlands in the free-flowing (FF1, FF2, FF3) and in the impounded stretch (IM1) for each hydrological condition. Different letters denote significant differences between wetlands (*p* < 0.05).



Fig. 3. Comparisons of phytoplankton, rotifer and microcrustacean  $\alpha$  functional diversity between wetlands in free-flowing (FF1, FF2, FF3) and impounded stretches (IM1), separately for post-flood and no flood sampling date. Different letters denote significant differences between wetlands (p < 0.05).



**Fig. 4.** Comparisons of β-functional diversity between wetlands for phytoplankton, rotifers and microcrustaceans in free-flowing (FF1, FF2, FF3) and impounded stretches (IM1) at post-flood and no flood conditions. Different letters denote significant differences among wetlands (p < 0.05).

The environmental heterogeneity was higher *between sections* than *between habitats* in wetlands in the free-flowing section, but similar across scales in IM1, where values were low and resembled those registered at the smaller scale in the FF wetlands (Fig. 5). Phytoplankton and rotifer functional  $\beta$ -diversities followed a similar pattern, with higher values *between sections* than *between habitats* in most of the FF wetlands. In the impounded stretch, differences across scales were registered only at no flood conditions (Fig. 5). Microcrustacean functional  $\beta$ -diversity was similar across scales for all wetlands (Fig. 5).

Regarding phytoplankton functional  $\gamma$ -diversity, the UTC was higher in FF3 and lower in IM1 for both hydrological conditions; the Rao's *Q* was higher in FF2 in high waters and similar among all wetlands for no flood condition. For rotifers, the UTC was higher in FF3 and IM1 for post-flood, and lower in FF2 in no flood conditions; Rao's *Q* was similar among all wetlands for post-flood, and higher in IM1 for no flood. For microcrustaceans, UTC values were higher in FF3 and IM1 than in FF1 and FF2 in both hydrological conditions; Rao's *Q* values were lower in FF2 for post-flood and similar values among all wetlands were detected in no flood condition (Table S2).

# 3.3. Functional composition

The PCA plots based on functional composition of phytoplankton showed a broader distribution of the sampling sites from wetlands in the free-flowing than from the impounded stretch for both hydrological conditions, as depicted by the aggregation of cross symbols (red polygon, Fig. 6). In IM1, for both hydrological conditions, the phytoplankton community was mainly composed of either large or medium sized organisms, flagellated (*Peridinium* spp., *Cryptomonas* spp.) or colonial (*Fragilaria* spp., *Pandorina* spp., *Pediastrum* spp.), with silica requirements (Cocconeis spp., Cyclotella spp., Navicula spp., Nitzchia spp.).; Cyclotella sp. was dominant at no flood conditions, when large filamentous species (Oscillatoria sp. and Phormidium sp.) were additionally present. Though several traits such as small size and colonial (Monoraphidium spp., Merismopedia spp.) were absent in IM1, these traits and all other traits were well represented in wetlands from the free-flowing stretch. Likewise, the composition of rotifers was more homogeneous and restricted to fewer traits in IM1 at post-flood conditions, when loricated, littoral and raptorial feeders with virgate or ramate trophi (i.e., Bdelloidea, Cephalodella spp., Lepadella spp., Colurella spp., Lecane spp. and Synchaeta spp.) dominated. All these traits were represented in wetlands from the free-flowing section, where pelagic, microphagous feeders with different trophic types and different body characteristics were additionally present (i.e., Keratella sp., Anaueropsis fissa, Polyarthra spp., Brachionus spp.). A similar pattern was observed at no flood conditions, except for one IM1 site, where the presence of Keratella (loricated with spines) broadened the functional polygon of composition in this wetland. Regarding microcrustaceans, in the IM1 sites small littoral organisms with different feeding strategies prevailed, like scraper feeders or with C or B-filtration type and herbivoredetritivore or omnivore-carnivore diets (i.e., Chydorus sp., Bosmina longirostris, Simocephalus spp., Alona spp., Thermocyclops oithonoides). In wetlands from the free-flowing stretch, these traits were also represented, and filter feeders with S and Sca-filtration types and herbivore and carnivore diets were additionally registered (Fig. 6).

# 4. Discussion

There is growing demand for multiscale studies planned to answer crucial questions concerning spatial patterns of diversity and how we



**Fig. 5.** Variations of  $\beta$ - functional diversity across scales:  $\beta 1$  (between habitats),  $\beta 2$  (between sections) for a) phytoplankton, b) rotifers and c) microcrustaceans in wetlands from free-flowing (FF1, FF2, FF3) and impounded stretches (IM1) for post-flood and no flood conditions.



**Fig. 6.** Biplots of PCAs based on trait composition for phytoplankton, rotifers and microcrustaceans for post-flood and no flood conditions. Phytoplankton traits: Akin, akinete; Aerot, aerotopes; Chl.b, chlorophyll *b*; Chl.c, chlorophyll *c*; Col., colonial; Fil, filamentous; Flagel, flagellate; Med, medium sized; Mixo, mixotrophic; Muci, mucilaginous; Nfix, nitrogen fixation; Sin.cel, single cell; Sireq, with silica requirements; X.lar, extra-large. Rotifer traits: BS, body size; Forcip, forcipate trophi; Incu, incudate trophi; IL, illoritcate; Litt, littoral; LO, loricated; LS, loricated with spines; Mall, malleate; Mallr, malleoramate; Microp, microphagous; Pelag, pelagic; Ram, ramate; Virg, virgate; Rapt, raptorial; Unci, uncinate trophi. Microcrustacean traits: Car, carnivorous; Herb, herbivores; Herb.det, herbivorous-detritivores; Fill, filterers; Fil.B, filtration type B; Fil.C, filtration type C; Fil.D, filtration type D; Fil.S, filtration type S, Fil.Sc, filtration type S, Color in this figure legend, the reader is referred to the web version of this article.)

human beings might improve our activities to preserve biodiversity (Gaston, 2000; McGill et al., 2015). In this study, we found that both phyto- and zooplankton functional diversity differed between wetlands in free-flowing and impounded stretches of the Danube River, and that such difference was affected by the hydrological condition. Post-flood conditions (i.e. high waters) promoted higher functional  $\beta$ -diversity for phytoplankton and rotifers in wetlands from the free-flowing

stretch, where environmental heterogeneity was also higher than in the impounded one. These differences were attenuated at no flood condition, when all wetlands presented more similar  $\beta$ -diversity values, no matter differences in environmental heterogeneity persisted. In general, these results agree with our expectations and with previous studies showing that the absence of a dynamic flooding regime altered the heterogeneity of floodplain habitats, contributing to biotic homogenisation (Braghin et al., 2018; Oliveira et al., 2018). Floods affect the influence of environmental gradients and promote plankton diversity as compared to scenarios with no floods (Nabout et al., 2007; Simões et al., 2013). Chaparro et al. (2018) found that the studied floodplain habitats were differently affected (or non-affected) by flood events during summer 2014, depending on their degree of connectivity and that the resulting environmental gradient probably favoured the differentiation of phytoplankton and rotifer communities along these wetlands. However, our present findings for no flood condition, when patterns of functional  $\beta$ diversity did not follow those of environmental heterogeneity, suggest that other factors may also influence species distribution in floodplain habitats; in this sense, Chaparro et al. (2018) indicated that such situations may be related to the spatial configuration of floodplain habitats, or the dispersal of organisms or contingency effects.

Our comparisons across spatial scales comprised a further step to depict that environmental heterogeneity and functional β-diversity were mainly related to the gradient of hydrological connectivity between water sections. Such gradient only occurs in wetlands from the freeflowing section, where water level is variable (Heiler et al., 1995). There, the broad range of environmental conditions (nutrient, suspended solid, DOC concentrations), favoured changes in the functional composition of rotifers and phytoplankton communities, in agreement with previous findings that reported changes of taxonomic composition along these wetlands (Baranyi et al., 2002; Schagerl et al., 2009). Contrarily, in the impounded stretch, the homogeneous influence of controlled, small river water inputs to all water sections (Edinger, 2009) may have determined more stable and similar environmental conditions (e.g. high dissolved nutrient concentrations) and plankton composition in all sampling sites. In FF3, where the hydrological connectivity is limited, intermediate responses of environmental heterogeneity between the more extensively restored (FF1 and FF2) and the IM1 wetland further support the idea of a crucial role of a dynamic hydrology as main generator of environmental variation (Hein et al., 2004; Funk et al., 2009; Baart et al., 2010). On the other hand, the higher similarity between patterns in FF3 and IM1 coincides with their nearer location and thus the influence of a spatial covariation along the river cannot be discarded.

Interestingly, we found an overall congruent response of functional and taxonomic (data not shown) diversity in our study. This indicates low levels of functional redundancy in these communities and emphasizes the importance of preserving the present state of the restored wetlands to guarantee no loss of ecosystem functions. As previously reported, damming of large rivers can cause functional homogenisation in its associated floodplains due to the loss of certain trait combinations at the community level (Braghin et al., 2018; Oliveira et al., 2018).

Even though  $\alpha$ -functional diversity (of rotifers and microcrustaceans in particular) is not lower or is even higher in the wetland in the impounded stretch (as compared to the free-flowing ones), the lower  $\beta$ -diversity indicates that some traits may have a lower chance to occur in any part of the whole wetland area. In this sense, some ecological traits prevailed in the impacted floodplain habitats, but others were nearly absent. The dominance of littoral rotifers with raptorial feeding mode in IM1 differs from previous findings in floodplain environments, where pelagic microphagous prevailed (José de Paggi et al., 2014; Chaparro et al., 2015). This may respond to the extensive macrophyte cover in all IM1 water sections, which was probably favoured by rather constant low flow velocity and the lack of disturbance by floods (Franklin et al., 2008; Baart et al., 2010). In the wetland from the impounded stretch phytoplankton was characterized by species typically thriving in slow-flowing enriched vegetated water, namely mixotrophic flagellated that can migrate in the scarcely mixed water column, ticoplanktic pennate and centric diatoms and cyanobacteria bearing aerotopes. In the free-flowing stretch, the broad range of environmental conditions also included wetland habitats with a high hydrological connectivity, frequent floods and periodically high flow velocities, representing suitable conditions for pelagic microphagous rotifers and small-sized (fast growing and opportunists) phytoplankton species, which were scarcely found in the impounded wetland. The near absence of such ecological strategies in impacted wetlands might affect the food web and important ecosystem functions such as nutrient cycling (Hébert et al., 2016); these important aspects still need further research.

Our multi-scale design combined with the comparisons between different planktic assemblages allowed us to depict that the response of the communities to environmental gradients occur at different spatial scales. This probably reflects that a definite suite of ecological traits determines differential species responses to environmental gradients at spatial scales. For example, the unexpected higher rotifer and microcrustacean  $\alpha$  diversity in IM1 than in FFs wetlands evidences that the absence of floods and flushing events, together with the habitat availability and refuge effect provided by macrophytes, allow for organisms with different traits to colonize and establish. Although such hydrological conditions would also be suitable for a variety of phytoplankton traits, extensive macrophyte development may have counteracted through competition for nutrients and light (Reckendorfer et al., 2013) and/or a top-down effect may have been taking place, as small palatable organisms were nearly absent in IM1. Similar values of microcrustacean β-diversity between FF and IM wetlands may respond to the fact that these organisms occur mainly at a narrow range of the environmental gradient offered by floodplain wetlands, which is present in both the impounded and free-flowing stretches. These relatively large and slow growing zooplankters dominate at low flow velocity conditions and non-disturbed habitats (Baranyi et al., 2002). In this sense, water sections with high or intermediate connectivity levels, frequent floods and high flow velocity (occurring only in FF wetlands) do not represent additional habitats for microcrustaceans and therefore, do not favour  $\beta$ -diversity for this group.

Lower  $\beta$ -diversity values in impounded (as compared to FF wetlands) result in decreased  $\gamma$ -diversity for phytoplankton but not for rotifers, which compensated with increased  $\alpha$ -diversity and resulted in similar  $\gamma$ -diversity among IM and FF wetlands. This knowledge is of major relevance as altered patterns of diversity may represent alterations in ecosystem functioning, such as phytoplankton primary production and nutrient cycling (Behl et al., 2011; Hébert et al., 2016).

# 5. Conclusions

We found that spatial patterns of functional diversity of phytoplankton, rotifers and microcrustaceans in floodplain wetlands from an impounded stretch of the Danube River are altered as compared to more pristine wetlands in a free-flowing stretch. Main differences occurred after a flood event that only affected FF wetlands, stressing the role of periodical flooding as driver of plankton diversity distribution. Comparisons across spatial scales highlight the relevance of the lateral gradient of hydrological connectivity as a main source of environmental heterogeneity leading to higher  $\beta$ -diversity. Our study contributes to a more comprehensive understanding of functional diversity distribution under the current state of human intervention of riverine floodplain systems. Taking into consideration the major importance of floodplain areas for the ecological integrity of large rivers, our results draw attention to the possible consequences of further alterations of flooding dynamics driven by human intervention together with climate change.

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