ORIGINAL ARTICLE

Lateral hydrological connectivity differentially affects the community characteristics of multiple groups of aquatic invertebrates in tropical wetland pans in South Africa

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Abstract

1. River–floodplain connectivity (i.e. lateral hydrological connectivity, LHC) can directly affect the community characteristics by promoting dispersal of organisms but can also have profound indirect effects by altering local habitat characteristics. A major challenge is to disentangle the relative importance of direct and indirect effects of LHC on organisms. Combining taxonomic data with trait information allows a more mechanistic understanding of how LHC affect biotic communities in floodplains.

2. Here, we attempted to determine the relative importance of the direct and indirect effects of LHC on local environmental variables and community characteristics (taxonomic and trait composition) of three different taxonomic organism groups in a set of 33 temporary floodplain pans along a gradient of LHC. In addition, we specifically aimed to unravel the underlying mechanisms shaping patterns of taxonomic diversity by partitioning compositional dissimilarity between ponds into components of nestedness and spatial turnover.

3. Variation partitioning revealed that most differences in macroinvertebrate and zooplankton community composition between pans resulted from variation in local environmental variables, particularly macrophyte cover and the presence of fish. For large branchiopod crustaceans, however, partitioning indicated that LHC did significantly affect both taxonomic and trait community composition, and reduced local taxon diversity. Partitioning taxonomic and trait β-diversity showed that community dissimilarity between pans was largely determined by turnover, rather than by nestedness.

4. Overall, our study revealed that the effects of LHC on aquatic invertebrate communities act mainly indirectly by altering local environmental conditions. Although the effects of LHC were significant, they were small compared to those of environmental variables.

5. Our results from the partitioning of taxonomic and trait β-diversity have important implications for biodiversity conservation efforts in the Ndumo region. We

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demonstrate the need to conserve multiple pans along the LHC gradient to sustain high regional diversity. A common practice in the study area mainly focuses on the conservation of river-connected or larger pans.

1 | INTRODUCTION

Habitat connectivity impacts metacommunity structure and dynamics of aquatic ecosystems by creating opportunities for organisms to disperse among habitat patches (Chase, 2003; Leibold et al., 2004). In the river floodplain ecosystems, hydrological regime is a key factor determining habitat connectivity between the river and its floodplain, thereby driving ecological functioning and biodiversity patterns of this system (Hayes et al., 2018; Junk, Bayley, & Sparks, 1989). Floodplain habitats strongly rely on natural patterns of lateral hydrological connection (LHC) between the river and floodplain to sustain resident biota and ecosystem processes such as organic matter decomposition and nutrient cycling (Friberg, Harrison, O'Hare, & Tullos, 2017; Junk et al., 1989). Earlier studies indicate that biodiversity in floodplains depends on the connection to the river, with relatively lower diversity at low LHC due to limited input of nutrients from the river and the lower dispersal probability (Thomaz, Bini, & Bozelli, 2007; Ward, Tockner, & Schiemer, 1999). Similarly, regular flooding promotes high LHC, leading to lower biological diversity due to dilution of floodplain conditions (e.g. nutrients) and homogenising effects through an influx of propagules (Conceição, Higuti, Campos, & Martens, 2018; Fischer, Bakevich, Shea, Pierce, & Quist, 2018; Ward et al., 1999). The highest levels of diversity in river floodplain systems are often observed at intermediate levels of LHC (Gallardo et al., 2014; Turić et al., 2015; Ward & Tockner, 2001). Empirical studies have shown that multiple organism groups including zooplankton, macroinvertebrates, fish, amphibians, and macrophytes tend to respond differently to variation in hydrological habitat connectivity (Frisch, Libman, D'surney, & Threlkeld, 2005; Morán-Ordóñez et al., 2015; Ward et al., 1999), which seems largely related to life history characteristics and dispersal mode (active versus passive). Active dispersing invertebrates might show in stronger responses to local environmental variables, indicating the importance of species sorting and habitat filtering, and a weaker response to LHC, whereas passive dispersing invertebrates might respond stronger to LHC (Dube et al., 2017; Hill, Heino, Thornhill, Ryves, & Wood, 2017; Li et al., 2019).

Lateral hydrological connection in the river floodplain ecosystems does not only promote the exchange of organisms between the river and floodplain wetlands. It may also have profound indirect effects on aquatic biota via altering local environmental conditions in wetlands (De Nooij, Verberk, Lenders, Leuven, & Nienhuis, 2006), for example by dilution of nutrients and dissolved salts (Junk et al.,

1989; Lizotte et al., 2012; Thomaz et al., 2007; Weilhoefer, Pan, & Eppard, 2008), or by bringing in sediments and organic matter from the river (Junk et al., 1989; Ward, Tockner, Arscott, & Claret, 2002). It is therefore expected that LHC can also have profound indirect effects on the characteristics of aquatic communities. Consequently, variation in LHC across wetlands (pans) might promote habitat variability at the landscape scale, which can result in higher regional diversity (De Nooij et al., 2006; Thomaz et al., 2007).

Previous studies demonstrate that the exchange of organisms in river–floodplain ecosystems largely depends on the floodplain distance to the river and the existence of hydrological connections between the river and the floodplain (Amoros & Bornette, 2002). Such systems are typically characterised by the occurrence of LHC, which implies that wetlands closer to the main river are likely to be more frequently connected to the river with a more frequent exchange of organisms, nutrients, and sediments with the river compared to more distant wetlands (Carlson, Fincel, Longhenry, & Graeb, 2016; Dube et al., 2017; Stoffels, Clarke, Rehwinkel, & McCarthy, 2013). Although the relative importance of the mechanisms by which LHC can determine local macroinvertebrate community characteristics in river and floodplain wetlands is well documented for multiple climatic regions (Gallardo et al., 2008; Paillex, Castella, & Carron, 2007; Tockner, Baumgartner, Schiemer, & Ward, 2000; Tockner & Ward, 1999), including subtropical (Arrington & Winemiller, 2006; Gallardo et al., 2014; Zilli, Montalto, & Marchese, 2008) and semi-arid regions (Sheldon, Boulton, & Puckridge, 2002; Sheldon & Thoms, 2006), knowledge on the impact of LHC on the structure and functioning of temporary floodplain wetlands in arid regions is rather limited. In temperate and subtropical regions, increased hydrological connectivity tends to reduce the complexity of invertebrate assemblage by reducing spatial heterogeneity (Gallardo et al., 2014; Zilli et al., 2008). In contrast, semi-arid regions are characterised by a strong fluctuation between being highly connected (i.e. during flooding) and disconnected (i.e. during drought or dry season) such that the degree of connection between water bodies might strongly impact community composition (Sheldon et al., 2002). For example, Sheldon et al. (2002) observed strong similarity in macroinvertebrate community composition between high and low connected systems.

Partitioning diversity into its α, γ, and β components is a frequently used approach to explore the spatial organisation of biodiversity at the landscape scale (Baselga, 2010; Crist, Veech, Gering, & Summerville, 2003). Alpha-diversity typically refers to the diversity

in a local habitat patch, whereas γ-diversity generally represents the total diversity in a set of habitat patches at the regional landscape scale (Jost, 2007; Sfenthourakis & Panitsa, 2012; Whittaker, 1960). Beta-diversity captures community differentiation among habitat patches. Nature conservation programmes typically aim at safeguarding high levels of regional diversity, which can only be achieved by having both high local diversity and high β-diversity (Socolar, Gilroy, Kunin, & Edwards, 2016). Beta-diversity can further be partitioned into its components of *nestedness* and *spatial turnover* (Baselga, 2010). Nestedness refers to the situation where species-poor sites are subsets of species richer sites (Almeida-Gomes, Rocha, & Vieira, 2016; Almeida-Neto, Guimarães, Guimarães, Loyola, & Ulrich, 2008; Ulrich, 2009), whereas spatial turnover indicates species replacement among habitat patches (Baselga, 2010; Koleff & Gaston, 2002; Qian, Ricklefs, & White, 2005). Partitioning β-diversity into its nestedness and spatial turnover components is effective to reveal causative processes that determine patterns of β-diversity (Baselga, 2010). The method is also highly relevant for applied biodiversity conservation (Berglund & Jonsson, 2003; Wright & Reeves, 1992). A dominance of nestedness suggests that regional biodiversity can be maintained by targeting conservation efforts towards a relatively small number of sites with high local diversity. In contrast, a dominance of spatial turnover indicates that the conservation of multiple sites is needed to maintain high levels of regional diversity (Baselga, 2010; Berglund & Jonsson, 2003).

Variation in community characteristics between habitat patches has traditionally been investigated mainly based on taxonomic information. Although such approaches have contributed strongly to our understanding of the processes determining community assembly, they are also limited by the fact that they only allow indirect interpretation of the potential mechanisms shaping variation in biological communities (Eros, Heino, Schemera, & Rask, 2009; Heino, Schmera, & Erős, 2013). More recently, there is an increasing interest in the integration of trait-based approaches into community ecology (Salguero-Gómez, Violle, Gimenez, & Childs, 2018; Weithoff & Beisner, 2019). Indeed, the analysis of traits allows a more mechanistic understanding of the factors determining variation in community characteristics (Bonada, Doledec, & Statzner, 2007; Verberk, Van Noordwijk, & Hildrew, 2013). The characterisation of trait–environment relationships might therefore gain a better mechanistic understanding of the responses of ecological assemblages to variation in environmental conditions.

The temporary floodplain wetlands (pans) of Ndumo Game Reserve (NGR) in South Africa are located along a strong gradient of LHC (Birkhead, Brown, Joubert, Singh, & Tlou, 2018; Breen, Furness, Heeg, & Kok, 1978) and thus provide an ideal opportunity to investigate the importance of LHC on aquatic invertebrate community characteristics. A recent study showed that aquatic macroinvertebrate diversity in hydrologically connected permanent floodplain pans in NGR is highest during controlled flooding from an upstream dam (Dube et al., 2017). A clear understanding of the mechanisms by which LHC affects invertebrate community characteristics in NGR could strongly contribute to effective biodiversity conservation

programmes in the region. Current conservation efforts in the region are largely directed towards larger (>1 ha), more permanent pans (Britz, Hara, Weyl, Tapela, & Rouhani, 2015; Tapela, Britz, & Rouhani, 2015), while small temporary pans with varying LHC are largely ignored.

The present study aims to investigate the direct and indirect effects of LHC on community composition and diversity of invertebrates in temporary pans in the South African NGR. We specifically aim to identify the key factors underpinning variation in community composition and diversity in temporary pans along a gradient of LHC to the Phongolo River. We use a combination of taxonomic data and trait information to obtain a mechanistic understanding of the role of LHC on variation in community characteristics. We also aim to disentangle the mechanisms underlying β-diversity by partitioning compositional dissimilarity across pans into components of nestedness and spatial turnover.

We hypothesise that LHC affects local aquatic invertebrate communities through facilitation of dispersal and by altering local environmental conditions. We expect that communities in temporary pans with contrasting LHC will differ in community composition due to differences in dispersal mode and capacity (active and passive) and the extent to which organisms can actively select suitable habitats. We therefore expect a stronger effect of environment in actively dispersing and selective macroinvertebrates. For the passively dispersing zooplankton and large branchiopods in turn, we expect that LHC mainly has an indirect effect by promoting dispersal of planktivorous fish from the river into the temporary pans.

2 | METHODS

2.1 | Study area

Ndumo Game Reserve (NGR) is a 10,117-ha protected area in the Phongolo floodplain in north-eastern Zululand in South Africa (Figure 1). It is a sub-tropical region with a mean annual temperature of 23°C and mostly summer rains (average annual precipitation 630 mm). Although NGR is relatively small compared to many other protected areas in South Africa, the reserve comprises a relatively large number of pans (both floodplain and endorheic pans). The term *pan* is used in our study region to identify depression and floodplain wetlands with a flat bottom (Ollis, Snaddon, Job, & Mbona, 2013; Ollis et al., 2015). The reserve has been defined as a Ramsar site, wetland of international importance for biodiversity conservation, in 1997 because of its exceptional biological diversity, which is closely linked to the presence of permanent and temporary wetland pans. Inundations of the temporary pans depend on seasonal rainfall and controlled flow releases from Pongolapoort Dam, located upstream of the floodplain, during the dry season (Heeg & Breen, 1982). Regular controlled flood releases from Pongolapoort Dam sustain the water needs of human communities that depend on floodplain resources (Britz et al., 2015; Heeg & Breen, 1982).
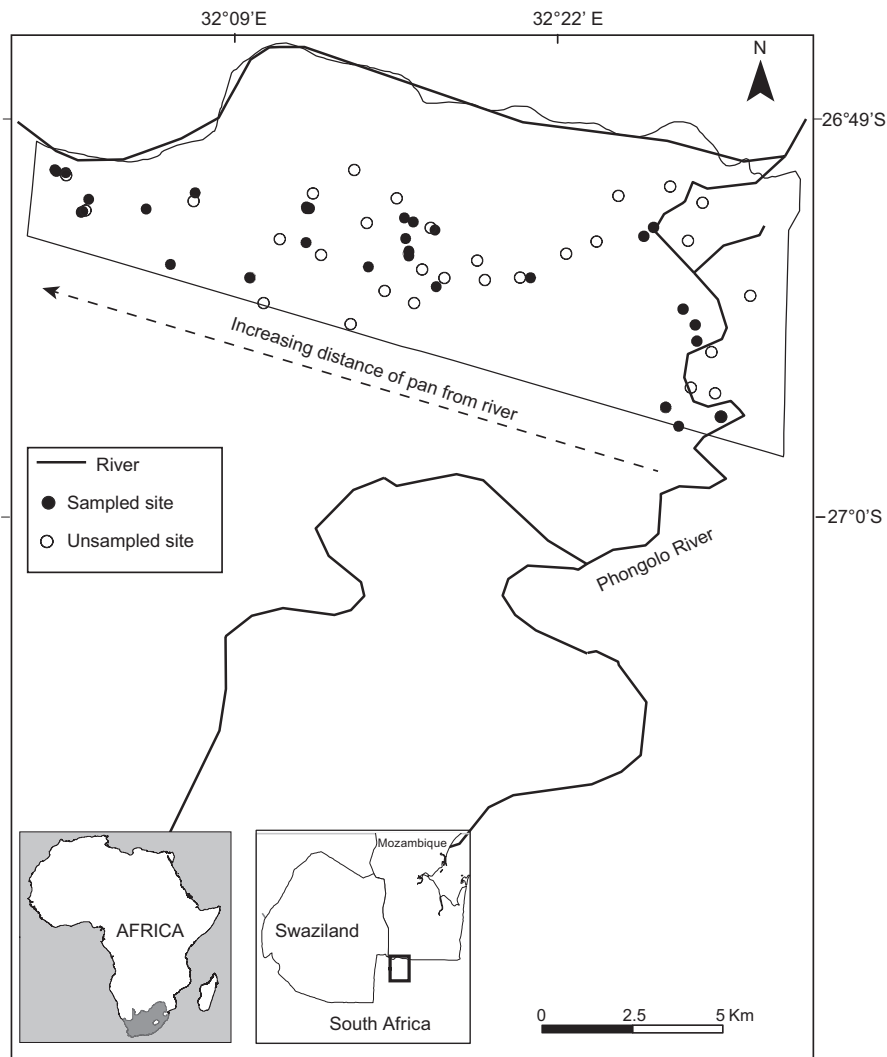
FIGURE 1 Temporary pans in the Ndumo Game Reserve. Black circles indicate sampled pans while hollow circles are similar pans that were not sampled. The dashed arrow represents the distance between pans and the Phongolo River, which is a good proxy for lateral hydrological connectivity between pans and the river. Larger distances between temporary pans and the river imply less frequent hydrological connectivity

2.2 | Sampling design

We investigated a set of 33 relatively small temporary pans in the Ndumo Game Reserve along a transect of increasing distance to the Phongolo River (i.e. 0.12–14 km; Figure 1). The selection of pans was largely done randomly, but accessibility of pans had to be taken into account as some a priori selected pans were completely inaccessible due to muddy conditions and very dense surrounding terrestrial vegetation. All investigated pans were located within a geographical area of 101.1 km² and were surrounded by natural grassland. The floodplain has a relatively low and uniform elevation from the river to the mainland, which results in a strong relation between LHC of pans and their distance to the river (Birkhead et al., 2018; Dube, Wepener, Van Vuren, Smit, & Brendonck, 2015). The set of investigated pans comprises a strong gradient in LHC, with pans close to the river having high LHC and pans far from the river low LHC. The most distant pans are never hydrologically connected with the river. The pans with the highest LHC in our study are connected to the river twice a year. The first connection occurs at the peak of the rainy season (February–March) and the second during the dry

season (September–October) when controlled floods are released from the upstream Pongolapoort Dam. The controlled floods are normally released once per year, except during occasional extended dry periods when water levels in Pongolapoort Dam are extremely low. All selected pans were visited once during the wet season of 2014 (February) to quantify environmental variables and to sample the macroinvertebrate communities. The negative distance of a pan to the river was used as a measure of LHC.

2.3 | Local habitat and environmental conditions

The surface area of each pan was determined with a handheld GPS eTrex30 (Garmin, U. K.) and the distance to the river in ArcGIS (10.2.2) based on geographic coordinates. The average water depth was measured once in each pan by taking depth measurements at 2-m intervals along the longest axis and perpendicular transects of the pan. Daytime oxygen concentration, water temperature, conductivity and pH were measured in situ with standard electrodes (IP67 combo meter, AZ Instrument Corp, Taiwan). Phytoplankton and cyanobacteria densities were estimated by measuring in vivo

concentrations of chlorophyll-*a* and phycocyanine using a hand-held fluorometer (*Aqua*Fluor, Turner Design, USA).

Depth-integrated water samples were collected with a tube sampler at multiple locations in each pan. Samples from different locations were pooled and subsamples were taken for later analysis of nutrient concentration (TN—total nitrogen, NO_3^-—nitrate, NO_2^-—nitrite, TP—total phosphate, NH_4^+—ammonium, PO_4^{3-}—phosphate) in the laboratory. Samples were kept at 4°C in the dark in the field and subsequently stored at −20°C in the laboratory until further analysis. Nutrient concentrations were assessed according to Dube et al. (2017).

The percentage of coverage with submerged, floating, and emergent aquatic vegetation was estimated visually and scored on an ordinal scale: (1: 1–25%, 2: 26–50%, 3: 51–75%, 4: 76–95%, and 5: 96–100%). The top layer of sediment (10 cm) was collected at multiple locations within each pan and pooled into one mixed sample. These samples were used to determine sediment carbon content after drying the sample at room temperature in the laboratory. The total sediment organic carbon was estimated following Nelson and Sommers (1996); (ASTM, 2000).

2.4 | Aquatic invertebrates

Aquatic macroinvertebrates and large branchiopods were sampled in each pan by sweeping a 500-µm D-frame kick-net 20 times across different micro-habitats, i.e. open water, submerged vegetation, emergent vegetation. This standardised semi-quantitative method allows direct comparison across pans. Samples were preserved in 5% neutral sodium phosphate buffered formalin and stained with Bengal Rose Dye. All macroinvertebrates were manually sorted from detritus in the laboratory using a stereo microscope (Olympus SZX12) and stored in 70% ethanol. The majority of specimens was identified to genus level following multiple macroinvertebrates identification keys (Day, Stewart, De Moor, & Louw, 1999), (Day, Harrison, & De Moor, 2002), (De Moor & Day, 2002; De Moor, Day, & De Moor, 2003, 2009). Hirudinae, Chironominae, Crambidae, Orthocladiinae, Nymphulinae, Dolichopodidae) were identified to family level and Oligochaetae were identified to order level.

Zooplankton was collected by filtering a space and depth integrated water sample of >80 L over a 64-µm mesh sieve. Samples were preserved in 70% ethanol and stained with a Bengal Rose Dye. Cladocerans were identified to species level under a stereo microscope (Olympus SZX12) following Day et al. (1999) and Van Damme, Bekker, and Kotov (2013) identification guides. We counted a minimum of 300 individuals for each sample. Copepods were grouped into calanoids and cyclopoids and counted. Ostracods were only counted. Information on the presence of fish in the pans was gathered from data collected in a separate fish survey of the Phongolo pans (de Swardt, 2015 unpublished data).

2.5 | Selection of species traits

Taxonomic data of invertebrates were complemented with taxon specific trait information reflecting the life history, mobility, morphology, and ecology of the aquatic invertebrates as obtained from the literature. We identified six relevant biological traits for invertebrates that relate to life history characteristics (development time, adult life stage, body size at maturity), mobility (swimming ability, dispersal mode) and feeding ecology (trophic niche) (Usseglio-Polatera, Bournaud, Richoux, & Tachet, 2000) (Table S2). The affinity of individual taxa with each trait was scored on an ordinal scale following Tachet, Ussegliopolatera, and Roux (1994) (Table S2). For trophic niche, lower scores indicate lower trophic feeders such as shredders while higher scores indicate higher trophic feeders such as predators.

2.6 | Data analysis

We first tested the extent to which LHC affected local environmental conditions in the pans and the community composition of each investigated organism group (macroinvertebrates, zooplankton, and large branchiopods) using separate redundancy analyses (RDA). Different organism groups were analysed separately because they are likely to show different responses to LHC due to diverging trait characteristics. Secondly, we used additional RDA to explore the effect of local environmental conditions and spatial descriptors on the community composition of each investigated invertebrate group. Environmental variables and spatial predictors that significantly contributed to observed variation in community composition were identified using a forward selection procedure following Blanchet, Legendre, and Borcard (2008).

Thirdly, we investigated the relative importance of direct and indirect effects of LHC and space on each investigated organism group separately, by applying multiple variation partitioning analyses based on partial redundancy analyses. The technique of variation partitioning allows to partition the total amount of variation explained by a statistical model into unique and shared effects of different sets of predictor variables (Peres-Neto, Legendre, Dray, & Borcard, 2006).

We included space (based on principal coordinates of neighbouring matrices [PCNM] spatial descriptors) as an additional explanatory variable set in the variation partitioning analyses because earlier analyses indicated that LHC was related to specific spatial predictors (Table S1). Spatial variables were generated based on the geographical coordinates of the pans using PCNM as described by Borcard and Legendre (2002). Principal coordinates of neighbouring matrices allows detection of spatial structure across a wide range of geographical scales (Borcard & Legendre, 2002; Dray, Legendre, & Peres-Neto, 2006). Principal coordinates of neighbouring matrices is an eigenvector-based technique that can be used to describe regular and irregular sampling designs. The geographical coordinates of the pans were used to construct an Euclidean distance matrix, which was subsequently truncated at the smallest distance that keeps all sites connected in a single network (2,889.8 m in the present study). The truncated Euclidean distance matrix was used in a principal coordinate analysis to extract eigenvectors associated with positive eigenvalues (19 out of 32), which we used as explanatory spatial variables in further statistical analyses. The PCNM produced orthogonal

maps that maximise the spatial auto-correlation (Borcard, Legendre, Avois-Jacquet, & Tuomisto, 2004; Dray et al., 2006) because of which PCNMs can be directly linked to the spatial patterns of the environmental variables and LHC.

The implemented variation partitioning analyses partition the amount of explained compositional variation across pans for each investigated organism group into seven different fractions: (1) a fraction uniquely explained by environment [E|S+LHC]; (2) a fraction uniquely explained by LHC [LHC|E+S]; (3) a fraction uniquely explained by space [S|E+LHC]; (4) a fraction of variation jointly explained by environment and LHC [E∩LHC]; (5) a fraction of variation jointly explained by environment and space [E∩S]; (6) a fraction of variation jointly explained by LHC and space [LHC∩S]; and (7) a fraction of variation jointly explained by environment, LHC, and space [E∩S∩LHC]. The interpretation of a significant unique effect of the explanatory variable set is straightforward and indicates a direct effect, independent of the other variables in the model. Shared effects may result from indirect effects with one factor having an effect through its impact on the other explanatory variable set, but can also result from an intrinsic correlation between explanatory variables. For example, shared effects of environment and LHC result from an indirect effect of LHC through its effect on local environmental conditions, whereas a shared effect between environment and space indicates an effect of spatially structured environmental variables. A significant shared effect between LHC and space refers to a direct effect of LHC and/or space. However, our model is not able to disentangle the unique contribution of both explanatory variables since they are to some extent related to each other (Table S1). Similarly, a shared effect between environment, LHC, and space suggests an indirect effect of LHC and/or space through their impact on local environmental conditions.
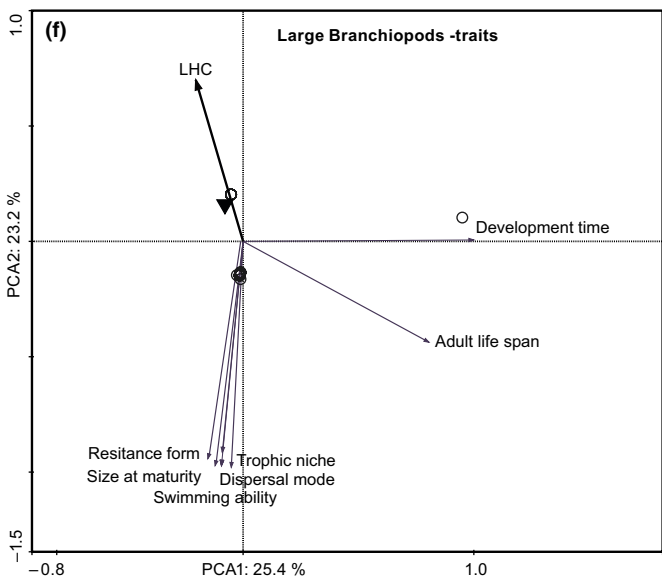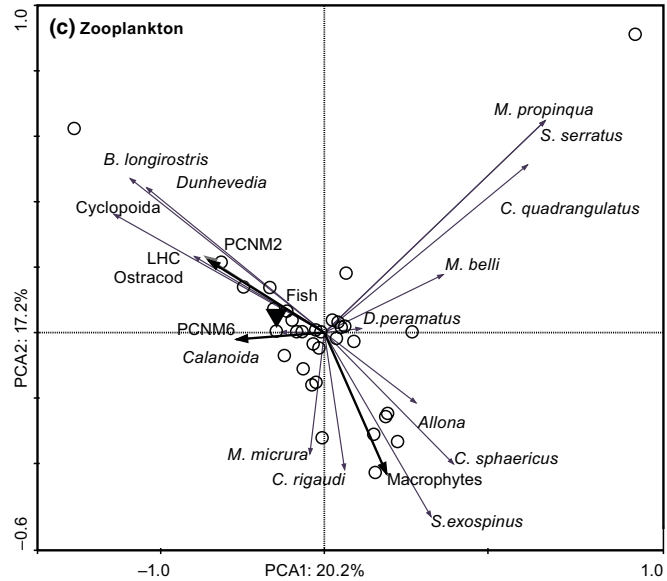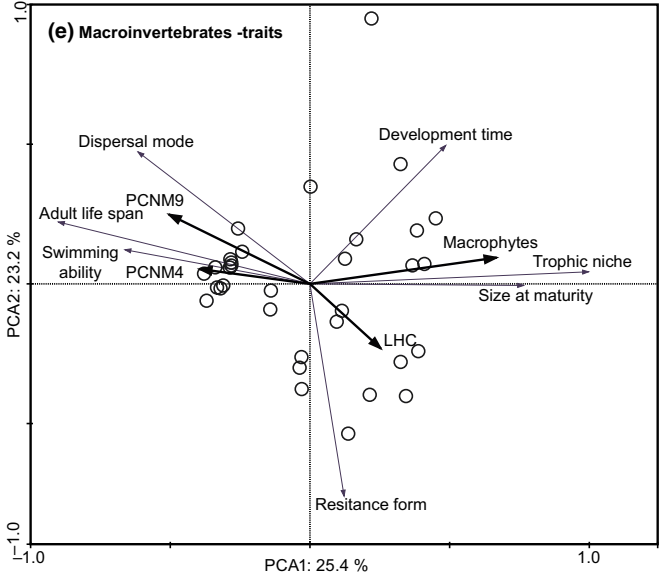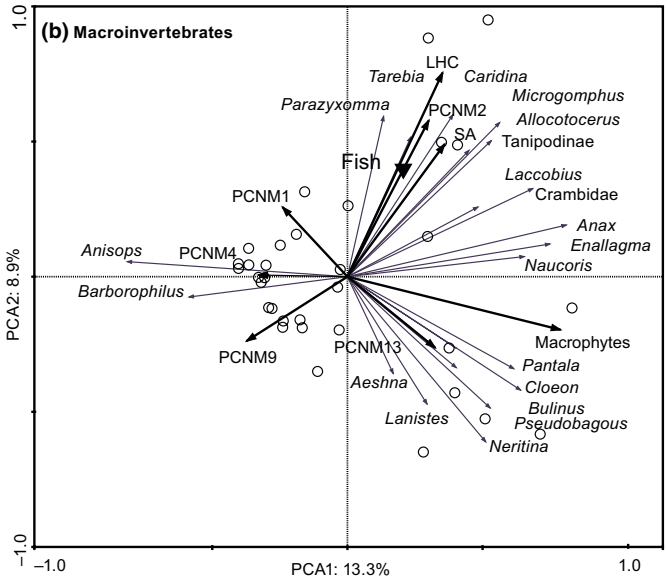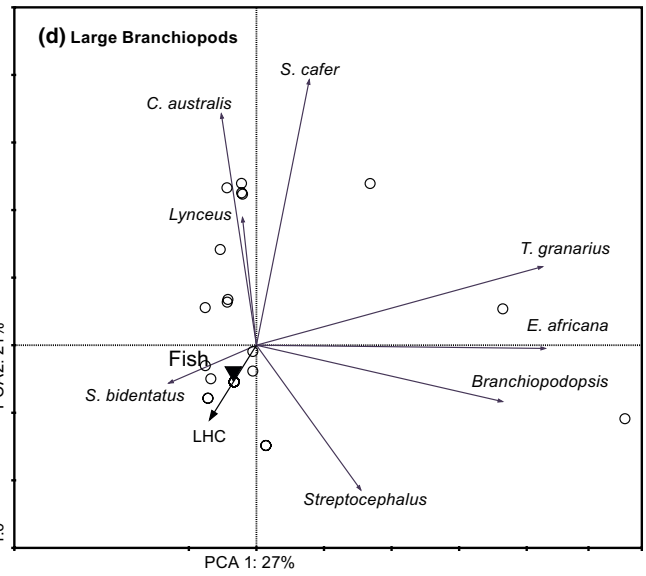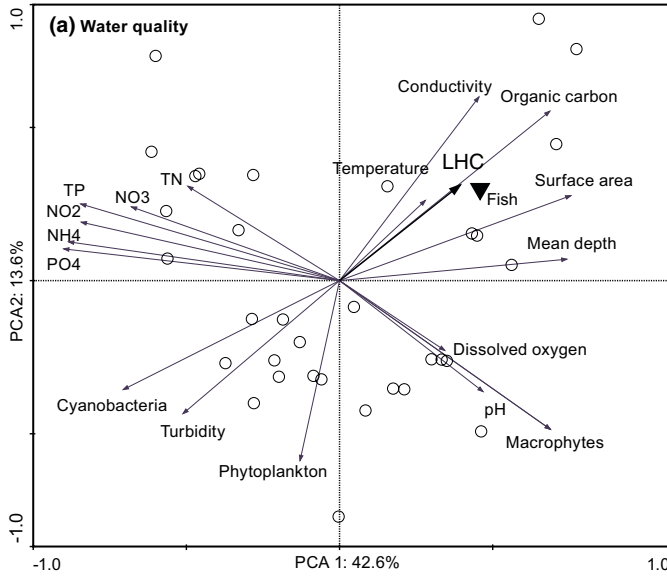
A similar approach with multiple RDA and variation partitioning analyses was used to test the unique and shared contributions of LHC, local environmental variables and space to variation in trait composition for each organism group separately. Prior to these analyses, we constructed a trait data matrix by weighing each trait by site specific taxon abundances ($\sum$ [(trait value × abundance of taxa)/abundance of organisms in each site]). Furthermore, the relationship between LHC and community traits was estimated using multiple separate Spearman correlations.

Taxonomic abundance data of all organism groups were Hellinger transformed prior to statistical analysis (Legendre & Gallagher, 2001). With the exception of pH, all local environmental variables were log transformed to improve normality of the data (Webster, 2001). The significance of the RDA models was assessed with Monte-Carlo permutations (n = 999). Associations between environmental variables

and LHC and between significant explanatory variables (LHC, PCNM predictors, and local environmental variables) and taxon composition were visualised using ordination plots of principal component analyses. The RDA and variation partitioning analyses were done in R using the *rda* and *varpart* functions, respectively (version 3.1.0, Oksanen et al., 2007) of the vegan package (Oksanen et al., 2016). Principal component analysis ordination plots were created in Canoco version 4.5 (Ter Braak, 1988).

In the second part of our analyses, we explored the distribution of aquatic invertebrate taxonomic diversity in NGR floodplain pans by partitioning diversity into its α, β, and γ components. Taxon richness was used as a measure of diversity. Gamma-diversity was defined as the total taxon richness of the entire set of sampled pans, whereas α-diversity represents the taxon richness in one pan. Beta-diversity of each organism group was defined as the compositional dissimilarity between pans and was calculated as the Baselga Jaccard (D_J) dissimilarity of species presence-absences (Baselga, 2010, 2012). In addition, we partitioned taxonomic and functional β-diversity into its turnover (Rep_B) and nestedness (Nes_{BJ}) components following Legendre (2014) and Villéger, Grenouillet, and Brosse (2013). *Turnover* here refers to the replacement of some species/traits by other species/traits from site to site, independent of potential differences in species/trait richness between the sites, whereas *nestedness* indicates differences in community composition produced by the differences in species/trait numbers (Baselga, 2010; Koleff, Gaston, & Lennon, 2003; Legendre, 2014). The composition of β-diversity was visualised with ternary plots using the SDR–simplex approach based on the Baselga index (Podani & Schnera, 2011). The partitioning of β-diversity was performed with the *beta.multi* function in R (version 3.1.0, Oksanen et al., 2007) of the betapart package (Baselga & Orme, 2012). We built a generalised linear model in R (version 3.1.0, Oksanen et al., 2007) using the *glm* function of the vegan package (Oksanen et al., 2016) to assess the impact of LHC on the presence of fish which was scored as a binomial variable (i.e. 0 = no fish and 1 = fish present). Lateral hydrological connection was included as a fixed continuous predictor and fish presence as a response variable in this model. Finally, the relation between α diversity with environmental variables and LHC was investigated through multiple regression models by first using the Akaike information criterion (AIC) to determine the best subset of variables. The normality of the residuals of regression models were tested using ShapiroWilk test (Wilk & Shapiro, 1965). The most parsimonious regression model was selected based on the model with the lowest AIC (ΔAIC> 2) (Burnham & Anderson, 2002). Prior to the multiple regression, correlation among explanatory variables was checked by

FIGURE 2 Ordination plot of principal component analysis (PCA) with (a) local environmental variables, taxonomic composition of (b) macroinvertebrates, (c) zooplankton, (d) large branchiopods, trait composition of (e) macroinvertebrates, and (f) large branchiopods. Lateral hydrological connectivity (LHC) was plotted as a supplementary variable to not influence the ordination. The black triangles represent centroid of fish presence. Black arrows represent significant local environmental variables, spatial descriptors, and LHC. Open circles represent samples. All explanatory variables were plotted as supplementary variables. For clarity, macroinvertebrate taxa that occurred in <25% of the samples are not visualised. Lateral hydrological connectivity, environmental variables, and space had no significant effect on variation in zooplankton trait community composition and an ordination plot showing the association between individual traits and explanatory variables is therefore not shown

(a) Water quality — PCA1: 42.6%, PCA2: 13.6%

(b) Macroinvertebrates — PCA1: 13.3%, PCA2: 8.9%

(c) Zooplankton — PCA1: 20.2%, PCA2: 17.2%

(d) Large Branchiopods — PCA 1: 27%, PCA2: 21%

(e) Macroinvertebrates -traits — PCA1: 25.4%, PCA2: 23.2%

(f) Large Branchiopods -traits — PCA1: 25.4%, PCA2: 23.2%

calculating Pearson correlations among variables. If variables were significantly correlated (Table S3), only the most relevant direct variable was retained.

3 | RESULTS

3.1 | The effect of LHC on local environmental conditions and invertebrate community composition

Redundancy analysis revealed that LHC affected local environmental conditions (R^2_{adj} = 0.08; p = .01) in the investigated temporary pans (Table S4). Pans with high LHC tended to be larger and deeper, and were characterised by a higher conductivity and by higher organic carbon content in the sediment. Pans with high LHC also had a lower turbidity and lower densities of phytoplankton and cyanobacteria compared to pans with lower LHC (Figure 2a). Additionally, high LHC was associated with the presence of fish (z = 2.63, p = .008; Figure S1). In contrast, nutrient concentrations were not associated with LHC. A summary of the environmental variables and morphometric measurements of the studied pans is provided in the supplementary information (Table S5).

Lateral hydrological connection also explained a considerable proportion of compositional taxonomic variation in the macroinvertebrate (R^2_{adj} = 0.04; p = .01), zooplankton (R^2_{adj} = 0.07; p = .001) and large branchiopod communities (R^2_{adj} = 0.09; p = .001; Table S4). Typical riverine macroinvertebrate taxa, such as the atyid shrimps *Caradina* sp., hydrophiloid beetles *Allocotocerus* sp., and *Berosus* sp., were positively associated with LHC (Figure 2b). Other macroinvertebrate taxa that were positively associated with LHC according to our analyses include the hydrophiloid beetles *Laccobius* sp., chironomid midges Tanypodinae, thiarid snails *Cloepatra* sp., gomphid dragonflies *Microgomphus* sp., and the libellulid dragonflies *Brachythemis* sp. Pans with high LHC had relatively more small zooplankton taxa such as *Bosmina longirostris*, *Dunhevedia* sp., and cyclopoid copepods, whereas larger bodied taxa such as *Simocephalus exospinosus* and calanoid copepods were more abundant in less frequently connected pans. Large branchiopods were absent in pans with high LHC.

Redundancy analyses showed that LHC did not have an effect on the trait composition of macroinvertebrates (R^2_{adj} = 0.02; p = .164), large branchiopods (R^2_{adj} = 0.0.5; p = .167) and zooplankton (R^2_{adj} = 0.08; p = .09) trait composition.

3.2 | Effect of local environmental variables and space on invertebrate community composition

Environmental variables significantly explained variation in taxonomic composition of macroinvertebrates (R^2_{adj} = 0.31; p = .001), zooplankton (R^2_{adj} = 0.19; p = .01), and large branchiopod communities (R^2_{adj} = 0.31; p = .001; Table S4, Figure 2b–d). Forward selection identified different sets of significant environmental variables for macroinvertebrates and zooplankton, but the presence of fish had a significant effect on the taxonomic composition of all investigated organism groups. Spatial descriptors explained a significant portion

of variation in the taxonomic composition of macroinvertebrate (R^2_{adj} = 0.27; p = . 005) and zooplankton communities (R^2_{adj} = 0.29; p = .007), but not of large branchiopod communities (R^2_{adj} = 0.004; p = .49). Different PCNMs representing the broad, intermediate, and fine spatial scale were selected for macroinvertebrates and zooplankton using a forward selection procedure (Table S4; Figure S3).

Environmental variables significantly explained the variation in community trait composition of macroinvertebrates (R^2_{adj} = 0.47; p = .002) and large branchiopods (R^2_{adj} = 0.20; p = .045), but had no significant effect on the trait compositional variation in zooplankton (R^2_{adj} = 0.12; p = .484). Spatial descriptors explained a significant proportion of variation in the trait composition of macroinvertebrates (R^2_{adj} = 0.53; p = . 008), but not in zooplankton and branchiopod trait composition (R^2_{adj} = 0.04; p = .891 and R^2_{adj} = 0.25; p = .178, respectively; Table S6).

3.3 | The relative importance of LHC, environment and space on invertebrate community composition

Variation partitioning analyses revealed that the overall effect of LHC on compositional taxonomic variation of investigated biota was relatively small. The effect of LHC acted largely indirectly through its impact on local environmental conditions (Figure 3). We observed no clear direct effects of LHC on macroinvertebrate and zooplankton community composition, but LHC seemed to have an important direct effect on the composition of large branchiopods. A considerable fraction of compositional variation in macroinvertebrate community was explained by shared effects between space and environmental conditions (Figure 3a). Compared to LHC and spatial variables, local environmental conditions tended to be more important for variation in taxonomic composition of the studied organism groups (Figure 3a–c). For macroinvertebrates and zooplankton, a considerable proportion of this variation was jointly explained by environment, space, and LHC and by environment and space. In addition, our analyses revealed a significant unique effect of space on the community composition of macroinvertebrates.

Variation partitioning analyses based on macroinvertebrate and large branchiopods trait community composition revealed similar pattern than with taxonomic community composition. Indeed, LHC did not significantly explain variation in trait community composition of macroinvertebrates, but had a significant effect on trait community composition in large branchiopod (Figure 3). A large proportion of the variation in macroinvertebrate trait composition was jointly explained by environmental variables (macrophytes) and space. In contrast, the unique effect of LHC, environmental variables, and space were not significant in explaining zooplankton trait composition. Separate Spearman correlations showed that LHC was positively associated with development time (Spearman: r's = 0.46, p < .01), resistance form (Spearman: r's = 0.38, p = .02), and size at maturity (Spearman: r's = 0.37, p = 0.03) of macroinvertebrates. For large branchiopods, LHC was negatively associated

FIGURE 3 Unique and shared contributions of local environmental variables (ENV), space and lateral hydrological connectivity (LHC) on the taxonomic composition of (a) macroinvertebrates, (b) zooplankton, (c) large branchiopods, trait composition of (d) macroinvertebrates and (e) large branchiopods. Asterisks indicate the significance level ***$p < .001$; **$p < .01$; *$p < .05$; and ns, not significant. Percentages represent explained variation by each component. The significance of shared contributions cannot be tested. Lateral hydrological connectivity, ENV, and space had no overall (marginal) effect on variation in zooplankton trait community composition and results are therefore not presented in Venn diagrams
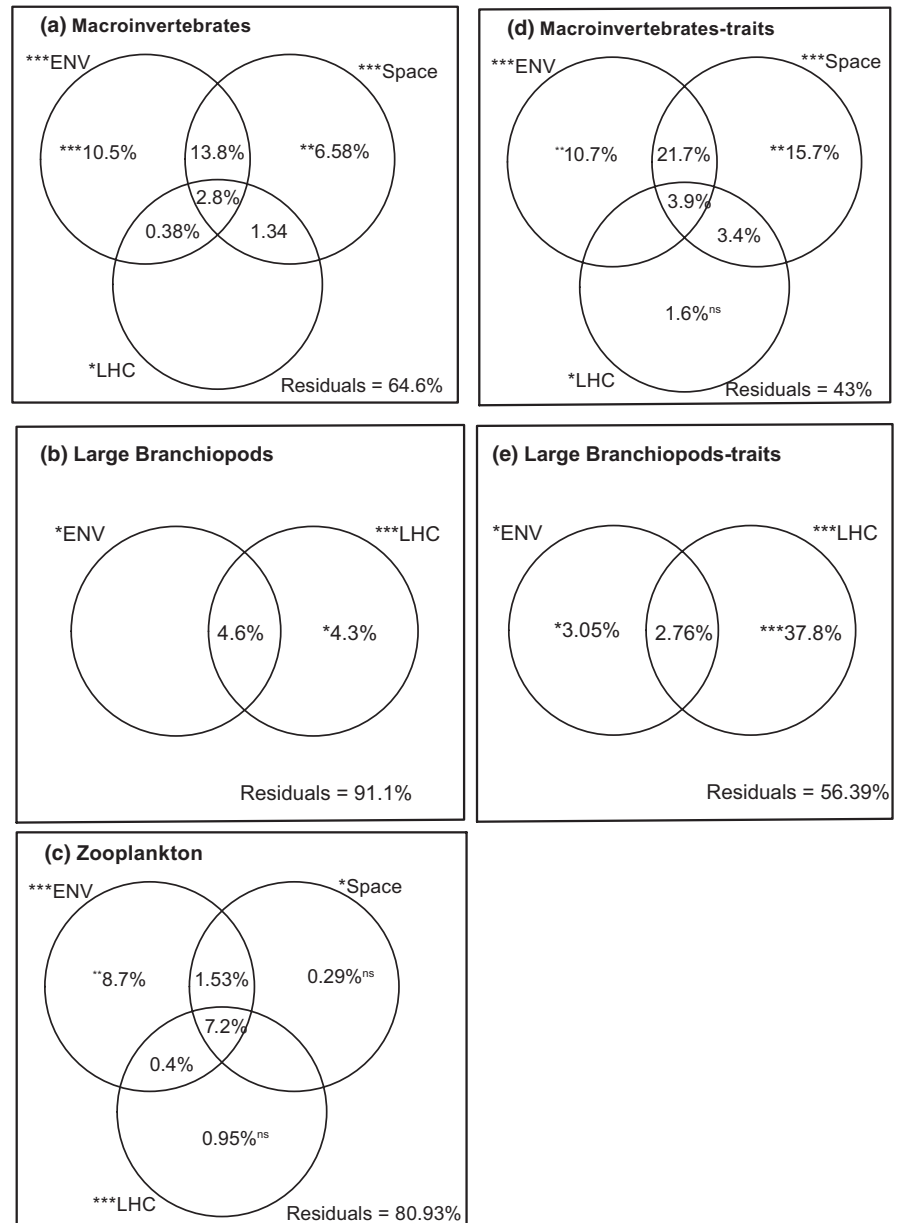
with development time (Spearman: r's = −0.59, $p < .01$), adult life stage (Spearman: r's = −0.54, $p < .01$), resistance form (Spearman: r's = −0.54, $p < .01$), swimming ability (Spearman: r's = −0.58, $p < .01$), dispersal mode (Spearman: r's = −0.54, $p < .01$), and trophic niche (Spearman: r's = −0.56, $p < .01$).

3.4 | Diversity measures in relation to environmental variables and LHC

The taxonomic richness of macroinvertebrates, zooplankton, and large branchiopods over the entire set of investigated pans was 78, 16, and 8, respectively (Table S7). The average α taxonomic richness in a pan was 17.36 (SD: ± 10.38), 4.3 (SD: ± 2.5) and 1.27 (SD: ± 1.38) for macroinvertebrates, zooplankton, and large branchiopods, respectively. Multiple regression analyses revealed that local richness

of both macroinvertebrates and zooplankton was positively associated by coverage with submerged macrophytes (Table S8). Local zooplankton richness was also positively correlated to total nitrogen concentration. There was no evidence for an effect of local environmental variables on the local richness of large branchiopods that were only observed in pans with low LHC. Beta-diversity was relatively low (D_J = 0.39; D_J = 0.36, and D_J = 0.39 for macroinvertebrates, zooplankton, and large branchiopods, respectively) and was mainly explained by spatial taxon turnover, rather than by nestedness (82 versus 18%, 79 versus 21%, and 83 versus 17% for macroinvertebrates, zooplankton, and large branchiopods, respectively; Figure S2). Similarly, trait β-diversity of macroinvertebrates was composed of spatial turnover rather than by nestedness. Spatial trait turn-over between pans was, however, smaller than taxonomic turnover between pans.

4 | DISCUSSION

We studied the effects of LHC on the taxonomic and trait community composition of aquatic macroinvertebrates, zooplankton, and large branchiopods in 33 temporary floodplain pans in the NGR in South Africa. As predicted by our hypotheses, we found a stronger direct effect of environmental variables on the macroinvertebrate taxonomic and trait composition. A direct effect of LHC on the taxonomic and trait composition was observed in large branchiopods. Partitioning of β-diversity revealed that variation in taxon occurrence among pans mainly resulted from spatial taxon turnover, rather than from nestedness. Overall, the results from this study improve our understanding on how direct and indirect effects of LHC structure invertebrate communities in subtropical floodplain wetlands in general and in temporary pans in particular.

4.1 | Effects of LHC on the taxonomic and trait community composition of aquatic invertebrates

Lateral hydrological connection directly explained a considerable fraction of variation in taxonomic and trait composition of large branchiopods but not of macroinvertebrate or zooplankton communities in NGR. In addition to a direct LHC effect, we also found evidence for strong indirect effects of LHC on large branchiopods as predicted by our hypothesis. The indirect effect of LHC on large branchiopods was probably due to the presence of predatory fish in temporary pans that are frequently connected to the river. In contrast, fish tended to be absent in most of the temporary pans with low LHC. The absence of fish in more disconnected temporary pans, may not only result from limited opportunities for fish to migrate into such systems, but also because of the usually shorter hydroperiod of endorheic pans that excludes fish without drought resistant life stages. The only exception was the occurrence of the killifish *Nothobranchius orthonotus* in one pan with low LHC. *Nothobranchius* species mature very fast and are capable to survive the dry period of temporary pans by producing drought resistant resting eggs (Pinceel et al., 2015; Williams, 2006).

Although large branchiopod crustaceans, such as *Triops* sp. and *Streptocephalus* sp. are good swimmers, they are mostly restricted to fishless waters because their large body size and active behaviour also makes them highly sensitive to visual predation by fish (Kerfoot & Lynch, 1987; Nhiwatiwa et al., 2009). While temporary waters are usually a safe refuge for large branchiopods, fish can temporarily invade floodplain systems during flooding events and eliminate the local vulnerable prey species. In this study, the large branchiopods were not observed in sites with high LHC. In addition to the effect on large branchiopods, fish can also alter the taxonomic composition of other wetland communities by positive size selective predation (Batzer, Pusateri, & Vetter, 2000; Hanson & Riggs, 1995). Indeed, several field studies have demonstrated that planktivorous fish predation caused a decrease in abundance of large cladocerans (e.g. *Daphnia*) while favouring small cladocerans (e.g. *Bosmina, Chydorus*), copepods, and rotifers (Ersoy,

Brucet, Bartrons, & Mehner, 2019; Jakobsen, Hansen, Jeppesen, Grønkjær, & Søndergaard, 2003). This is in line with our study where, small bodied zooplankton species, such as *Bosmina longirostris*, *Dunhevedia* sp. dominated the sites with fish, while larger bodied taxa such as *Simocephalus exospinosus* were more abundant in pans without fish. Other studies found a positive association between the presence of fish and aquatic invertebrate life habits (e.g. semi-sessile and burrowing) because the lower mobility associated with such traits leads to a lower exposure and reduces their chance to be preyed upon (Boelter, Stenert, Pires, Medeiros, & Maltchik, 2018; Gathman, 2019).

A number of species have evolved adaptations to better cope with the presence of fish in their habitats, either through predator avoidance or by adaptive traits that reduce susceptibility to predation. For instance, some active dispersers (e.g. Coleoptera) are able to perceive the presence of fish by detecting kairomones in the water and can, as such, avoid sites with fish (Resetarits, 2001). Permanent inhabitants of temporary waters, such as zooplankton species, can modulate their hatching behaviour in the presence of fish cues and refrain from hatching when fish kairomones signal the presence of predatory fish (Lass, Vos, Wolinska, & Spaak, 2005; Nielsen, Smith, Hillman, & Shiel, 2000; Pinceel et al., 2015). A similar hatching behaviour towards predation by turbellarian flatworms is known for large branchiopods (De Roeck, Artois, & Brendonck, 2005). If a similar response takes place towards the presence of fish needs further investigation. It is therefore possible that, although some zooplankton and large branchiopod taxa were absent in our active samples, they could have been present in the resting egg bank, awaiting predator-free conditions to hatch.

Since visually hunting fish species predominantly predate on larger individuals and species (Drenner, Dodson, Drenner, & Pinder Iii, 2009; Laske, Rosenberger, Kane, Wipfli, & Zimmerman, 2017; Wellborn, Skelly, & Werner, 1996), fish predation often drives a shift to smaller taxa and can lead to reduced average body sizes within the invertebrate community. Indeed, our results show a positive association between fish presence with size at maturity for macroinvertebrates. The observed negative association between adult life span and development time of large branchiopods with LHC in our study might be indicative for the shorter hydroperiod of pans with low LHC that selects for taxa that mature fast. Although we do not find evidence for an overall effect of LHC, environment and space on variation in trait community composition of zooplankton, our analysis based on taxonomy shows a shift towards smaller bodied taxa (e.g. cladocerans such as *Bosmina longirostris*, *Dunhevedia*, and cyclopoid copepods) of fish. This is in line with earlier investigations on the impact of predation by fish on zooplankton (Lemmens, Declerck, Tuytens, Vanderstukken, & De Meester, 2018; Mamani, Koncurat, & Boveri, 2019).

The observed significant unique effect of space on macroinvertebrate community composition suggests that macroinvertebrates are to some extent dispersal limited. This finding is in line with previous studies on freshwater pond clusters that highlight the importance of hydrological connections as dispersal pathways for

aquatic insects (Oertli, Indermuehle, Angélibert, Hinden, & Stoll, 2008; Van De Meutter, De Meester, & Stoks, 2007). However, it should be noted that these unique effects in our study might also derive from the effect of unmeasured spatially structured variables. In contrast to macroinvertebrates, no significant unique effect of space emerged for zooplankton. This suggests that zooplankton is not dispersal limited in our study region. Our findings are consistent with earlier observations demonstrating increasing impact of dispersal limitation in macroinvertebrates with increasing body size (De Bie et al., 2012). While many macroinvertebrate taxa depend on specific traits for active dispersal (Elizabeth, Storey, & Smith, 2017; Rodil et al., 2017), zooplankton largely rely on passive dispersal by vectors including flowing water, wind, birds, and large mammals (Havel & Shurin, 2004; Incagnone, Marrone, Barone, Robba, & Naselli-Flores, 2015; Vanschoenwinkel, Gielen, Vandewaerde, Seaman, & Brendonck, 2008). Ndumo Game Reserve is an important bird area and home to small and large bodied vertebrates that make use of wetlands for drinking and/or wallowing, which may contribute to rapid dispersal of zooplankton resting eggs. Also, during massive flooding events, dormant zooplankton stages may be transported among habitats. Natural floods usually occur at the start of the wet season, when pools are newly inundated and many macroinvertebrate taxa are not yet present. Zooplankton and large branchiopod resting eggs, however, can be eroded from the pond sediment and dispersed between habitats (Bilton, Freeland, & Okamura, 2001; Cohen & Shurin, 2003).

As LHC was to some extent related to space in our study, we could not fully disentangle the unique effects of LHC and space on community and trait composition of the investigated invertebrate groups. However, it is very unlikely that this limitation undermines the key findings of our study. Only a relatively small fraction of explained variation is shared between space and LHC for macroinvertebrates, which is suggestive of direct effects of LHC and/or space. Some of the variation in macroinvertebrate and zooplankton community composition that was jointly explained by LHC and space was also shared with environment, suggesting indirect effects of LHC and/or space via the environment. This pattern could be realised through effects of LHC on environmental variables and/or because environmental variables were spatially structured. Overall, we can confidently conclude that the indirect effects of LHC were more important than the direct effects in structuring the community and trait composition of the studied organisms.

The amount of unexplained variation in community composition was relatively high, especially for large branchiopods. This may be due to two main reasons. First, our study is based on a single sampling event in-time of only the active community and does not capture relevant temporal variation in community characteristics, which is often linked to temporal variation in environmental conditions (Botwe et al., 2015; Hutchinson, 1961). Second, it is very likely that we did not quantify all important variables. For example, inundation length was not measured but has previously been shown to be an important driver for community assembly (Boven & Brendonck, 2009; Hill et al., 2016; Waterkeyn, Grillas,

Vanschoenwinkel, & Brendonck, 2008). In addition, a certain amount of unexplained variation might also result from the relatively coarse resolution of taxonomic identification. Finally, our standardised sampling of active communities may be incomplete in space and time in the sense that we may have missed individuals and/or taxa.

4.2 | Aquatic invertebrate diversity

Local environmental conditions were important in explaining macroinvertebrate and zooplankton diversity in the NGR temporary wetlands, especially through the presence and abundance of macrophytes. Lateral hydrological connection negatively affected the local diversity of macroinvertebrates and large branchiopods, probably as a consequence of fish predation, supporting findings from similar studies (Nhiwatiwa, Brendonck, Waterkeyn, & Vanschoenwinkel, 2011; Schilling, Loftin, & Huryn, 2009).

Taxonomic and trait β-diversity of the investigated organism groups were mainly composed of turnover between pans rather than by nestedness. This finding has important implications for invertebrate diversity conservation in NGR. Based on our results, it is therefore recommended that conservation measures should not only focus on more or less river-connected pans or on larger pans only, a common current practice in the study area. Our study underlines the importance of maintaining pans of different sizes along the entire LHC in order to sustain a high regional species richness. Also, former studies stressed the importance of maintaining different water bodies with varying size along environmental gradients to sustain high levels of regional biodiversity (Hooper et al., 2012; Leibold, Chase, & Ernest, 2017).

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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