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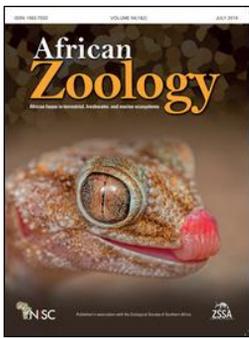
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A comparison of aquatic macroinvertebrate and large branchiopod community composition between temporary pans of a conservation area and surrounding communal area in South Africa

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Although temporary wetlands are often biodiversity hotspots that deliver multiple ecosystem services, they are also threatened by human exploitation. We conducted a comparative field study to investigate the impact of reserve protection on the diversity and community structure of aquatic macroinvertebrates of temporary wetlands (pans) in South Africa. Specifically, we compared the diversity and community composition of macroinvertebrates with a special focus on large branchiopod crustaceans in pans of a protected nature reserve (Ndumo Game Reserve) with that of pans in the surrounding anthropogenically disturbed area (Ndumo Communal Area). Our results show that reserve protection has a significant positive effect on the diversity and community structure of the aquatic macroinvertebrates. The taxon diversity for macroinvertebrates in general and large branchiopods in particular was significantly higher in the Ndumo Game Reserve, compared with the Ndumo Communal Area. Overall, our results illustrate the need for continued protection of reserve areas and pans in this tropical region in South Africa for the conservation of macroinvertebrate species.

Keywords: anthropogenic disturbance, diversity, floodplain, Ndumo Game Reserve, wetlands

Supplementary material: available at <https://doi.org/10.1080/15627020.2020.1724827>

Introduction

Temporary wetlands constitute the majority of surface waters in arid and semi-arid regions (Brendonck and Williams 2000). Their particular hydroperiod (i.e. duration of the wet phase) depends on the local climate, soil characteristics and basin morphometry (Williams 2006). Despite their often relatively small size, temporary wetlands have the capacity to support local and regional aquatic biodiversity with high numbers of endemic species (Ferreira et al. 2012; Nhiwatiwa et al. 2014). Temporary wetlands may represent biodiversity hotspots in human dominated landscapes, such as urban, communal and agricultural areas (Van den Broeck et al. 2015a). However, temporary wetlands are also vulnerable to human effects, including pollution, drainage and land use intensification (Nhiwatiwa et al. 2017).

In dry regions across Africa, where rainfall is limited, temporary wetlands are a major source of water for agricultural and household use (Scoones 1991). Although temporary wetlands may therefore provide essential resources to human communities, intensive exploitation can change their biodiversity and functioning (e.g. nutrient cycling and carbon sequestration). This, in turn, may

undermine the long-term delivery of important ecosystem services (including water source) (Williams 2006). Previous studies on temporary wetlands have reported significant effects of land use on water quality variables (e.g. nutrients and conductivity) (Bird and Day 2014) that impact the aquatic communities of these systems (Schell et al. 2001). For example, agricultural activities and deforestation in the proximity of wetlands often results in higher total nitrogen and phosphorus concentrations (Declerck et al. 2006). Grazing and trampling by farm animals or wildlife, in turn, may cause direct physical damage (Declerck et al. 2006; Dalu et al. 2017) or enhance eutrophication through defecation or resuspension of nutrients from the sediments (Declerck et al. 2006).

The ecological importance of aquatic macroinvertebrates in South Africa is often underappreciated, because they are generally small and inconspicuous. Still, they may be an important link in the food chain between primary producers and consumers at higher trophic levels, such as fish, birds and amphibians, by mediating break-down of organic matter, nutrient cycling, bioturbation and acting as prey themselves (Macadam and Stockan 2015). For example, many bird

species rely on macroinvertebrates in wetlands as a food source (Guillemain et al. 2000; Whittington et al. 2013).

Information on the community composition and diversity of aquatic invertebrates can be used to assess the status and ecological integrity of wetlands (Chessman et al. 2002). The aquatic invertebrates are a highly diverse group that is relatively easy to sample and in which multiple taxa vary considerably in their sensitivity to environmental stressors (Van den Broeck et al. 2015b). Specific habitat quality indicators, based on the occurrence and diversity of macroinvertebrate taxa, have therefore been developed for river systems in Africa e.g. South African Scoring System (SASS) (Dickens and Graham 2002) and Tanzanian River Scoring System (TARSIS) (Kaaya et al. 2015). Macroinvertebrates are also increasingly being used in different regions as biomonitoring tools to determine water quality in wetlands (Ferreira et al. 2012; Bird et al. 2013; Van den Broeck et al. 2015b; Bird et al. 2019). Permanent inhabitants of temporary wetlands, such as large branchiopods, in particular have potential as focal groups, because they are exclusive to these systems (Nhiwatiwa et al. 2014; Bird et al. 2019).

Information on the effect of anthropogenic activities on wetland ecosystems is crucial for current environmental policymaking. A profound knowledge of the association between biodiversity and environmental conditions, and an improved understanding of how these relate to anthropogenic activities is essential for the development of effective conservation programs that enforce sustainable exploitation of natural ecosystems. In South Africa, much progress has been made towards a framework for the assessment of the ecological integrity (Ollis and Malan 2014; Bird and Day 2016) and development of policy for the sustainable utilisation of wetlands (NWA 1998). Comparative studies focusing on both biotic and abiotic wetland characteristics in anthropogenic disturbed and protected areas within the same geological region are needed to fill in current knowledge gaps, particularly for temporary wetlands. The temporary pans in Ndumo, South Africa, present an ideal opportunity to study the effects of reserve protection on the community characteristics of aquatic macroinvertebrates by comparing macroinvertebrate communities in pans in the protected Ndumo Game Reserve (NGR) with those from pans located in the neighbouring and anthropogenically disturbed Ndumo Communal Area (NCA). The large branchiopods were reported separately in this paper from the other macroinvertebrates, because in many areas of the world, including our study area, large branchiopod diversity, species composition, and conservation status remains largely unknown (Brendonck et al. 2008; Nhiwatiwa et al. 2014; Mabidi et al. 2016; Bird et al. 2019). In addition, large branchiopods are considered as 'flagship species' of temporary aquatic water bodies and deserve special attention (Brendonck et al. 2008). Flagship species are here defined as species selected to act as a symbol for a defined habitat (Hermosillo-Núñez et al. 2018).

The aims of the present study are to determine the differences in (i) macroinvertebrate and large branchiopod diversity and community composition and (ii) environmental conditions in the pans between NGR and NCA in the

Phongolo River floodplain in KwaZulu-Natal, South Africa. In addition, we aim to explore to what extent differences in macroinvertebrate and large branchiopods community composition and diversity are related to variation in environmental conditions between NGR and NCA. We also aim to highlight the most important environmental variables that explain the diversity and community composition of macroinvertebrates and large branchiopods in the studied pans. Overall, we expect that anthropogenic activities in the NCA significantly affect the environmental conditions of pans and the diversity and community composition of aquatic invertebrates. Therefore, we expect that protection of the pans by the reserve is important to maintain the regional macroinvertebrate diversity.

Materials and methods

Study area

Ndumo Game Reserve (NGR) and Ndumo Communal Area (NCA) are located in north-eastern KwaZulu-Natal, South Africa (Figure 1). The region is subtropical with a mean annual temperature of 23 °C and mostly summer rains (mean annual precipitation 630 mm). Ndumo Game Reserve is a 10 117-hectare protected area that is part of the Phongolo River floodplain. Although NGR is small, compared with many other protected areas in South Africa, the reserve comprises a large number of temporary wetlands that are locally referred to as pans (Ollis et al. 2015). The temporary pans in NGR are relatively pristine, because of the protection that is offered by the reserve. Outside of the reserve, in the communal area (NCA), the temporary pans are exposed to anthropogenic effects, such as drainage for irrigation, grazing by communal animals and dumping of waste. As a result, bare ground is common in NCA in close proximity to the pans (100 m radius) and the vegetation is characterised by open wood and grassland. In addition, croplands are common around (and even in) the temporary pans in NCA (Dube pers. obs.). Inundations of these temporary pans depend on seasonal rainfall (endorheic pans) and controlled flow releases from the Pongolapoort reservoir (floodplain pans), located upstream of the floodplain, during the dry season (Dube et al. 2015). In this study, 38 endorheic pans were selected.

Local environmental conditions

The 38 temporary pans (27 in NGR and 11 in NCA) were sampled during the wet season in February 2014. The surface area of each pan (site) was estimated with a handheld GPS eTrex30 (Garmin) by tracking the circumference. The average water depth was determined 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 with standard electrodes (IP67 combo meter, AZ Instrument Corp).

Phytoplankton and cyanobacteria densities were estimated by measuring *in vivo* concentrations of chlorophyll-*a* and phycocyanine with a hand-held fluorometer (AquaFluor, Turner Design). The coverage of submerged, floating and emergent aquatic vegetation was estimated

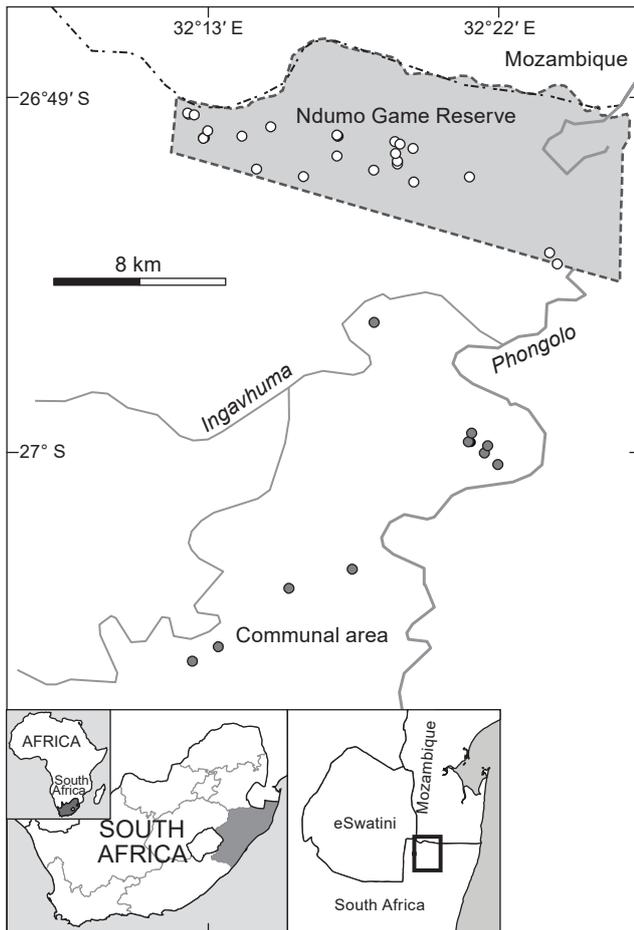


Figure 1: Map of the study area showing the location of sampled temporary pans in Ndumo Game Reserve (NGR) (white circles) and Ndumo Communal Area (NCA) (grey circles)

visually and scored on an ordinal scale: (1: 1–25%, 2: 26–50%, 3: 51–75%, 4: 76–95% and 5: 96–100%) (Nhiwatiwa et al. 2017). The assessment of macrophyte cover was done by one person throughout the sampling period to minimise observer bias.

Depth integrated water samples were collected with a tube sampler at multiple locations (5–10, depending on the size of the pan) in each pan. Samples from different locations were pooled and 1 l subsamples were taken to determine nutrient concentrations (TN, NO_3^- , NO_2^- , TP, NH_3^+ and PO_4^{3-}) in the laboratory. Samples were kept cool and dark in the field and stored at -20°C in the laboratory. Analyses were performed within seven days after sample collection. Nutrient concentrations were assessed from unfiltered water samples by spectrophotometry using Merck Spectroquant test kits (MA, Germany).

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 microhabitats, i.e. open water, submerged vegetation, emergent vegetation. This standardised semi-quantitative method allows direct

comparison across pans (Biggs et al. 1998; Hill et al. 2016). Samples were preserved in 5% neutral sodium phosphate buffered formalin and stained with Bengal Rose Dye. All macroinvertebrates were manually sorted from detritus and other debris in the laboratory using a stereo microscope (Olympus SZX12) and stored in 70% ethanol. The majority of specimens was identified to genus level using various invertebrate identification keys and guidelines for southern African species (Day et al. 1999; Day et al. 2002; de Moor et al. 2003; Stals and de Moor 2007; de Moor et al. 2009), except for Crambidae, Dolichopodidae, Hirudinae, Nymphulinae, Orthoclaadiinae, Stratiomyidae, Tabanidae, Syrphidae and Tanyptodinae that were identified to family level.

Data analysis

Effect of reserve protection on environmental variables in NGR and NCA

Principal component analysis (PCA) was used to visually explore the variation in local environmental variables between pans and their mutual relation in the NCA and NGR. Redundancy analysis (RDA) was used to formally test for the effect of Reserve Protection (RP) in the investigated pans. In this analysis, reserve protection (pan located in NGR or NCA) was defined as a dummy variable. Multiple additional univariate *t*-tests were used to test for differences between the NGR and NCA pans for each environmental variable separately. The variation of each measured variable was estimated using the standard deviation from the mean. The environmental variables were log transformed prior to statistical analysis to better approach a normal distribution of the residuals.

Effect of reserve protection on macroinvertebrate and large branchiopod richness and community composition

Taxon richness was defined as total number of taxa in each pan and gamma richness representing total number of taxa in both NGR and NCA. Gamma taxon richness were estimated with taxon accumulation curves (i.e. number of taxa as a function of number of sites) with Chao2 estimate (Chao et al. 2009). Firstly, the sample-based rarefaction curves were plotted separately for NGR and NCA to predict the taxon richness of sites and to estimate the number of taxa that would be found if sampling effort was reduced to a specified number of sites. Secondly, a combined sample-based rarefaction curve (NGR + NCA) was plotted to explore whether a combined taxon diversity differs from individual regional taxon diversity (i.e. NGR or NCA). Regional taxon richness at each site was estimated as the asymptote of the taxon accumulation curve. Chao2 estimates the asymptote of the taxon accumulation curve by taking into account the effect of rare species on total richness and may provide a better estimate of true taxon richness for small numbers of samples (Chao et al. 2009). To assess differences in macroinvertebrate and large branchiopod taxon richness between NGR and NCA pans, univariate *t*-tests were used after log-transformation of taxon diversity data, in order to better approach a normal distribution of the residuals (Webster 2001). We corrected

the variation in taxon richness and environmental variables for differences in sample size between NGR and NCA by using a resampling procedure taking averages of 11 random samples from 50 inventories using the *sample* function in R version 3.5.1.

Effect of environmental variables on taxon diversity and community composition

Associations between environmental variables and taxon diversity were investigated through multiple regression models and using the Information Criterion (AIC) to determine the best model. The most parsimonious regression models were then selected, based on the models with the lowest AIC ($\Delta\text{AIC} > 2$) (Burnham and Anderson 2002). Detrended Canonical Correspondence Analysis (DCCA) revealed that the gradient lengths of environment and community composition were rather short (< 3), which allows the use of linear methods (PCA/RDA) in our study (Šmilauer and Lepš 2014). We then used RDA analysis on Hellinger transformed abundance data, in order to test the extent to which (i) local environmental conditions and (ii) RP affects macroinvertebrate and large branchiopod community composition separately. Significant environmental variables were identified using forward selection following Blanchet et al. (2008). The significance of the RDA models was assessed with Monte-Carlo permutations ($n = 999$). Associations between significant explanatory variables and taxon composition were visualised using ordination plots of PCA. The significant explanatory variables were plotted as supplementary variables on the PCA plot. The DCCA and RDA's were performed with the *decorana* and *rda* functions, respectively, in R version 3.5.1, of the *vegan* package (Oksanen et al. 2016). To avoid collinearity of explanatory variables, the variance inflation of each factor in regression models were tested with function *vif* part of *car* (Fox and Weisberg 2011) and *VIF* (Lin et al. 2011) packages.

Mantel correlogram analysis

A Mantel correlogram analysis was performed to quantitatively assess the scale of spatial autocorrelation (Legendre et al. 2015). In this analysis, three matrices were used: a community dissimilarity matrix, based on Hellinger distances calculated using the abundance of each species in each pan, a spatial distance matrix, based on geographical coordinates of pans and an environmental Euclidean distance matrix, based on the environmental variables that significantly explained variation in community structure that emerged from forward selection models. The Mantel correlogram was calculated to test the relation between species and spatial distance matrices. The significance of Mantel statistic was tested using 1 000 permutations (Legendre et al. 2015). Then, to correct for the potential effect of spatially structured environmental variables explaining spatial autocorrelation in community composition, a partial Mantel analysis was performed following Legendre and Fortin (1989) testing for the effects of spatial distance on community composition, while correcting for environment. Finally, the spatial Mantel correlations were plotted as a function of geographical distance classes among the studied pans. The Mantel

correlogram analysis was performed with the *mantel correlog* function in R version 3.5.1, which is part of the *ecodist* package (Goslee and Urban 2007).

Relative importance of the reserve protection and environmental variables on macroinvertebrate and large branchiopod communities

We investigated the effect of RP on macroinvertebrate and large branchiopod community composition, independent of variation in local environmental conditions, by applying variation partitioning analyses, based on partial redundancy analyses (pRDA) (Legendre 2007). A pRDA allows the total variation that is explained by a statistical model to be partitioned into two or more groups of explanatory variables to identify their unique and shared contributions to total variance (Peres-Neto et al. 2006). We partitioned the amount of explained compositional variation of macroinvertebrate and large branchiopod communities between RP and significant environmental variables (E). Variation was partitioned into three different components: (1) the unique effect of environment ($E | RP$), estimating the direct effects of environmental variables, independent of reserve protection, (2) RP ($RP | E$), estimating the direct effects of reserve protection, independent of environment, and (3) the shared variation between reserve protection and environmental variables ($RP \cap E$), estimating the indirect effects of reserve protection through its effect on environmental variables. The variation partitioning analysis was performed with the *varpart* function in R version 3.5.1, which is part of the *vegan* package (Oksanen et al. 2016).

Results

Effect of reserve protection on environmental conditions in temporary pans

Local pan environmental variables varied between NGR and NCA (Table 1). From the PCA, the first two principal components explained 76% of the total variance in environmental variables in NGR and NCA (Supplementary Figure S1). The first component (PC1) explained 53% of the total variance and had a strong positive loading ($p > 0.05$) of nutrients (PO_4^{3-} , NO_2^- , NO_3^- , TP and TN) and negative loading of macrophytes and cyanobacteria (Supplementary Table S1). The second component (PC2) explained 23% of the total variance, had positive loading ($p > 0.05$) of temperature and dissolved oxygen (Supplementary Table S1). Separate *t*-tests demonstrate significant differences of five out of sixteen environmental variables between NCA and NGR pans. NCA pans were generally deeper ($t = 3.28$, $p < 0.05$), less turbid ($t = 2.36$, $p < 0.05$), and had significantly lower concentrations of PO_4^{3-} ($t = 2.34$, $p < 0.05$), NO_2^- ($t = 3.39$, $p = 0.006$) and NO_3^- ($t = 3.59$, $p < 0.05$), compared with pans in NGR. Redundancy analyses (RDA) did not reveal an overall significant effect of RP ($F_{1,36} = 1.04$, adjusted $R^2 = 0.02$, $p > 0.05$) on local environmental variables of the investigated temporary pans.

Aquatic invertebrate richness and community composition in temporary pans of NGR and NCA

The pans in NGR had a mean local macroinvertebrate taxa richness of 17.6 (SD: ± 2.5) and the mean local richness

Table 1: Pairwise comparisons of environmental variables (mean \pm standard deviation) between temporary pans from NGR and NCA. Significant levels are indicated by ** $p < 0.01$; * $p < 0.05$

Variable	NGR	NCA
Mean depth (cm)	11.19 \pm 1.9**	23.25 \pm 12.7**
Surface area (m ²)	533.39 \pm 365.0	705.20 \pm 971.6
Turbidity (NTU)	373.81 \pm 116.5*	246.10 \pm 168.1*
Cyanobacteria ($\mu\text{g l}^{-1}$)	8.79 \pm 1.8	8.67 \pm 7.4
Chlorophyll a ($\mu\text{g l}^{-1}$)	449.10 \pm 61.9	459.76 \pm 197.4
Total nitrogen (mg l ⁻¹)	4.52 \pm 0.7	5.65 \pm 2.5
Total phosphorous (mg l ⁻¹)	0.97 \pm 0.3	1.20 \pm 1.1
NH ₄ ⁺ (mg l ⁻¹)	1.29 \pm 0.3	1.42 \pm 1.3
PO ₄ ³⁻ (mg l ⁻¹)	2.85 \pm 0.9*	1.98 \pm 1.6*
NO ₃ ⁻ (mg l ⁻¹)	28.26 \pm 4.3*	18.24 \pm 10.7*
NO ₂ ⁻ (mg l ⁻¹)	0.64 \pm 0.2*	0.30 \pm 0.2*
Temperature ($^{\circ}\text{C}$)	29.41 \pm 0.8	33.67 \pm 4.9
pH	7.35 \pm 0.1	7.59 \pm 0.8
Dissolved oxygen (mg l ⁻¹)	4.64 \pm 0.7	6.78 \pm 4.2
Conductivity ($\mu\text{S cm}^{-1}$)	184.65 \pm 63.7	235.84 \pm 100.1
Macrophyte cover (%)	50 \pm 27.8	62 \pm 38.1

in NCA pans was 13.8 (SD: \pm 7.6), but this difference was not significant ($t = 2.13$, $p > 0.05$). However, the variation in macroinvertebrate taxon alpha richness among pans was higher in the set of NCA pans, compared with the NGR pans. In total, eight large branchiopod species were found over the entire set of studied pans. The pans in NGR had a significantly higher large branchiopod species richness; 1.73 (SD: \pm 1.61), compared with 0.18 (SD: \pm 0.4) in NCA (Mann-Whitney $U = 45$, $p < 0.05$). The highest number of large branchiopod species coexisting was five in one pan of NGR, whereas the majority of pans (31 out of 38) had at least one species. In contrast, two pans in NCA each had a single large branchiopod species, whereas large branchiopods were absent from the majority of pans (nine out of eleven). The estimated macroinvertebrate gamma richness (Chao2 estimate based on the same number of samples) in NGR and NCA was 66 and 48, respectively (Figure 2a). For large branchiopods, estimated gamma richness for NGR and NCA was six and two, respectively.

RDA revealed that RP had a significant effect on the macroinvertebrate ($F_{1,36} = 1.77$, $R^2_{\text{adj.}} = 0.02$, $p < 0.05$) and large branchiopod ($F_{1,36} = 2.26$, $R^2_{\text{adj.}} = 0.03$, $p < 0.05$) community structure. When all pans in NGR were pooled together, 34 macroinvertebrate taxa exclusively occurred in NGR pans, whereas eight taxa only occurred in NCA pans (Supplementary Table S2). The most abundant macroinvertebrate taxa in NGR were *Anisops* (39.7%), *Bullinus* (6.5%), *Lestes* (6.4%), *Enallagma* (5.8%) and *Cleon* (5.3%). *Anisops* and *Bullinus* occurred in 100% and 74% of the sampled pans. The rare taxa in NGR were *Hydroglyphus* (0.03%), *Anaciaeschna* (0.04%), *Haliphus* (0.04%), *Hydrochus* (0.04%), *Marocoris* (0.04%), *Naboandelis* (0.04%), *Parasthetops* (0.04%), *Dineutus* (0.03%), Dolichopodidae (0.02%), *Lymnaea truncatula* (0.02%), *Rhagadotarsus* (0.02%). In NCA, the most abundant taxa were *Anisops* (50.49%), *Enallagma* (7.8%), *Pantala flavescens* (6.13%) and *Bullinus* (5.36%). Rare taxa were *Berosus* (0.07%), *Bezzia* (0.07%), *Eretes* (0.07%), *Hydroglyphus* (0.07%), *Hydrovatus* (0.07%), *Mansonia*

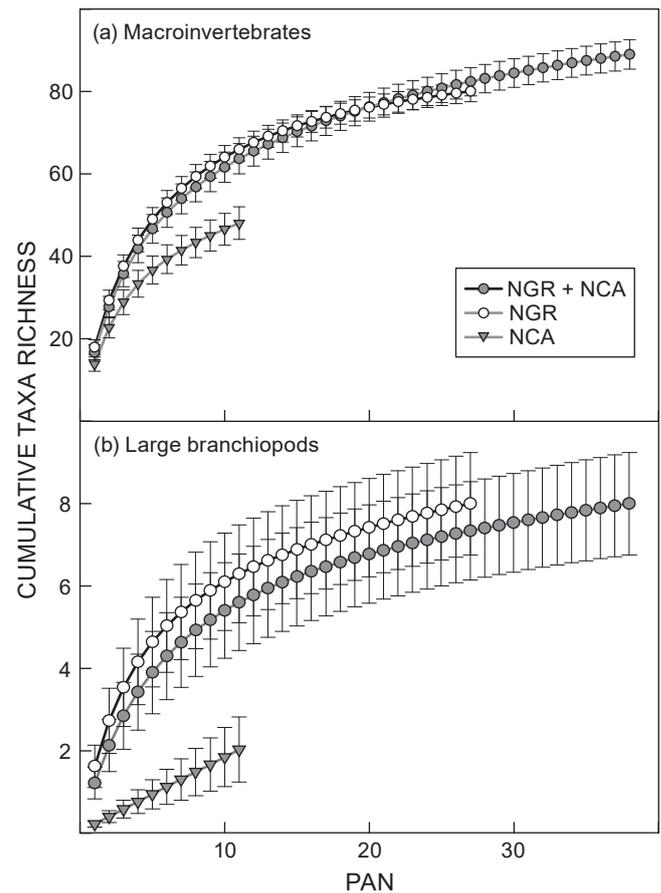


Figure 2: Species accumulation curves for (a) macroinvertebrates and (b) large branchiopods for 38 pans (study sites) in Ndumo Game Reserve (NGR) and Ndumo Communal Area (NCA) plotted as a function of number of sites sampled, by using the Chao2 estimate of species richness. Error bars indicate standard deviation of the mean

(0.07%), *Nerthra grandicollis* (0.07%), *Nychia limpida* (0.07%) and Syrphidae (0.07%). The abundant large branchiopods in NGR were *Streptocephalus cafer* (63.87%) and *Eulimnadia africana* (10.27%), whereas *Branchipodopsis* (0.09%) and *Leptestheria* (0.09%) were rare.

Effect of local environment on community diversity and composition

Macroinvertebrate taxon richness was positively associated with macrophyte cover, whereas large branchiopod species richness was negatively associated with water conductivity (Table 2). RDA revealed that macrophyte cover and oxygen concentration influenced the community composition of macroinvertebrates ($F_{5,33} = 1.81$, $R^2_{\text{adj.}} = 0.08$, $p < 0.05$), whereas macrophyte cover and conductivity had a significant effect on the community composition of large branchiopods ($F_{5,33} = 1.69$, $R^2_{\text{adj.}} = 0.07$, $p < 0.05$) (Figure 3).

Spatial autocorrelation of variables

Mantel correlogram analysis confirmed significant positive spatial autocorrelation of species composition up to a distance of 2 000 m (distance class 1: 0–1 900 m,

Table 2: Results of the general linear models with the most important variables explaining the macroinvertebrate (MI) and large branchiopod (LB) taxon richness. Values in bold indicate significant variables

Model and source	Estimate	Standard Error	t-value	Pr (> t)
Environment variables				
MI taxa richness ($R^2_{adj.} = 0.29$, $F_{3,34} = 6.28$, $p < 0.002$)				
<i>Chlorophyll a</i>	0.10	0.13	0.68	0.50
Dissolved oxygen	-0.06	0.13	-0.49	0.63
Macrophytes	0.19	0.04	4.28	0.001
LB taxa richness ($R^2_{adj.} = 0.09$, $F_{1,36} = 5.06$, $p = 0.03$)				
Conductivity	-0.76	0.33	-2.24	0.03

$r = 0.15$, $p < 0.05$ (Figure 4). This indicated that pans separated by 2 000 m or more significantly differ in species composition. Partial Mantel tests, correcting for environmental distances, showed significant spatial autocorrelation at distances of 3 000 m, distance class 1: 2 580–5 161 m: $r = 0.37$, $p < 0.05$; distance class 5: 10 321–12 982 m: $r = -0.53$, $p < 0.05$ and distance class 8: 18 063–20 643 m: $r = 0.37$, $p < 0.05$ (Figure 4).

Impact of reserve protection on macroinvertebrate and large branchiopod community structure

Variation partitioning revealed that the environment uniquely explained a significant proportion of variation in macroinvertebrate community composition ($R^2_{adj.} = 6.9\%$, $p < 0.05$), whereas reserve protection only accounted for 1.5% of the total variation. The shared variation between environmental variables and reserve protection was very small (0.5%). In contrast, the unique reserve effect significantly accounted for 2.2% of the large branchiopod variation, whereas the unique effect of environment was not significant and accounted for 2.0%. The unexplained variation for both macroinvertebrates and large branchiopods was relatively high (91.1% and 94.7%, respectively).

Discussion

The effect of reserve protection on taxon richness and environmental conditions in NGR and NCA

We found an overall effect of RP on large branchiopod and macroinvertebrate taxon richness. The observed higher large branchiopod taxon richness in protected pans is consistent with findings from similar studies where protection of wetlands by nature reserves promoted large branchiopod richness (Ferreira et al. 2012; Nhiwatiwa et al. 2014), whereas other studies show some weaknesses in the capacity of protected areas to protect aquatic macroinvertebrates (Guareschi et al. 2015; Zamora-Marín et al. 2016). This is because the criteria to designate protected areas is at times unrelated with aquatic biodiversity or reserves may contain aquatic environments that show no particularly rich macroinvertebrate communities (Zamora-Marín et al. 2016). Still, the threats posed by anthropogenic activity to conservation of species have been a key motivator for conservation biologists to develop protected areas where activities, such as agriculture, are officially excluded (Saraiva et al. 2018). Anthropogenic effects through the transformation of the

landscape around wetlands (e.g. cropland, livestock overgrazing or forest removal) pose a significant risk to the richness of wetland species (Ferreira et al. 2012; Dalu et al. 2017). Transformation of the surrounding land affects wetland hydrology, promotes siltation, contributes to eutrophication or degrades large areas of the wetland where extensive drainage occurs. Such environmental alterations then often lead to a decrease in species diversity (Best et al. 1993).

The observed variation in macroinvertebrate and large branchiopod richness in our study was largely mediated by variation in macrophyte coverage across pans. Our results revealed that taxon richness was positively associated with macrophyte cover. Macrophyte cover generally has a positive effect on aquatic biodiversity (Declerck et al. 2005) by enhancing the physical habitat structure, which enhances food availability and provides shelter against predators (Jeppesen et al. 1998).

Reserve protection did not have an overall effect on the environmental conditions of the temporary pans. In our study, the variability of some environmental conditions (e.g. TN, TP, cyanobacteria and phytoplankton) among pans in NCA was high, indicating the different levels of anthropogenic activities in the proximity of the pans. This idea is supported by the fact that terrestrial vegetation surrounding pans in NCA differed extensively among pans. The majority of pans in NCA were surrounded by bare ground, which is in strong contrast to NGR where pans were surrounded by grasses and trees. Furthermore, some pans close to homesteads in NCA were more frequented as a water source by livestock (Dube pers. obs.). Our results showed that the total phosphates and nitrogen were not significantly high in NCA, compared with NGR. It is noted that wildlife in NGR may likewise affect nutrient levels of temporary pans. The reserve indeed has a high density of small mammals, such as *Tragelaphus* sp. (Nyala), *Cephalophus natalensis* (Red Duiker), *Aepyceros melampus* (Impala), *Tragelaphus sylvaticus* (Bushbuck) and *Neotragus moschatus* (Suni), as well as large mammals, such as *Syncerus caffer* (Buffalo), *Diceros bicornis* (Black Rhino) and *Ceratotherium simum* (White Rhino), that frequent temporary pans for drinking and wallowing. In both cases, nutrient enrichment in and around the pans is possible through animal waste that may build up leading to subsequent water quality problems. Similar studies on natural wetlands and artificial watering points have demonstrated nutrient enrichment of wetland

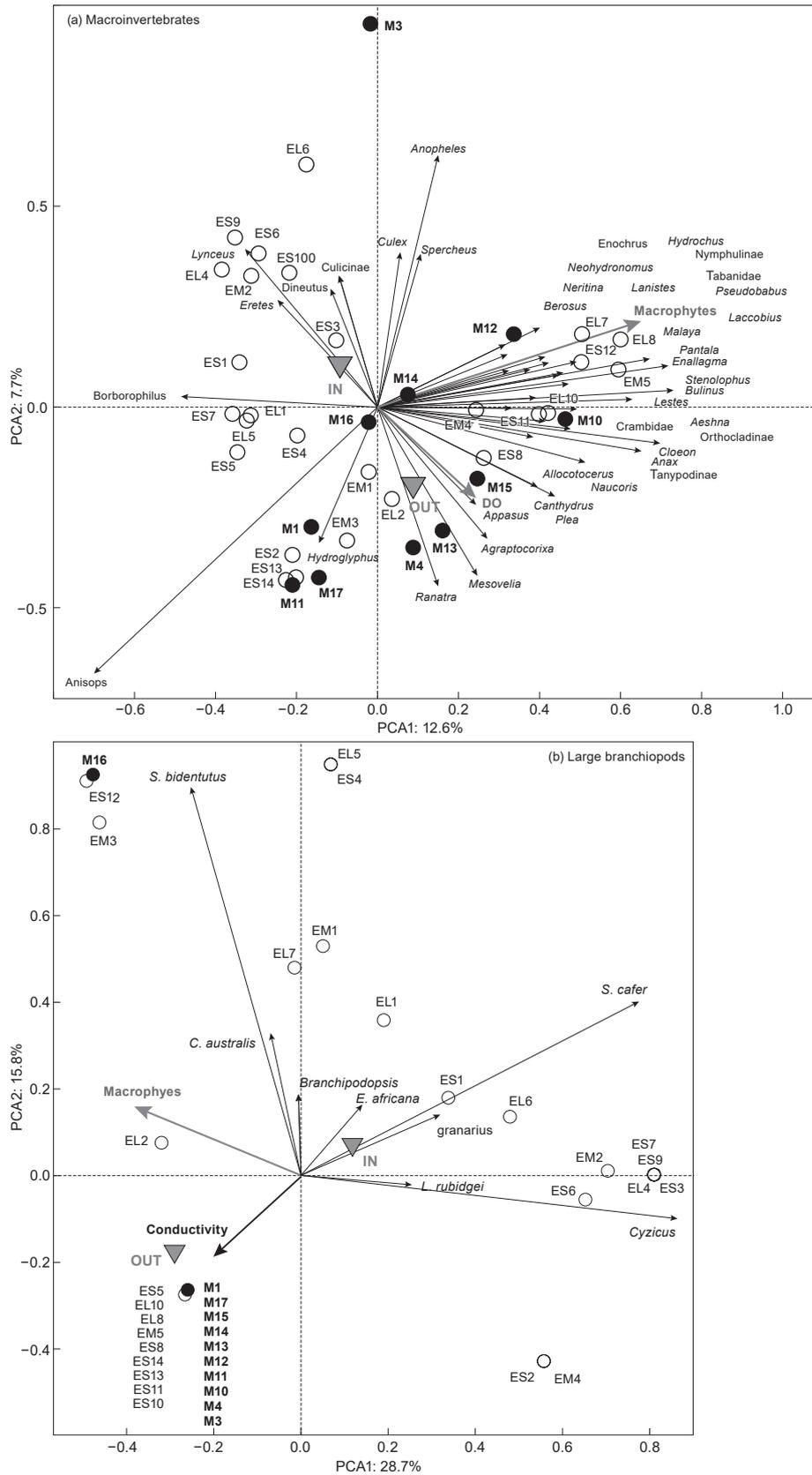


Figure 3: PCA ordination plot of the community composition of a) macroinvertebrates and b) large branchiopods. Black arrows represent significant local environmental variables. Empty and filled circles represent samples from Ndumo Game Reserve (NGR) and Ndumo Communal Area (NCA), respectively. All explanatory variables were plotted as supplementary variables. DO: Dissolved oxygen, IN: inside NGR and OUTNCA. For reasons of clarity, macroinvertebrate taxa that occurred in less than 15% of the samples are not shown

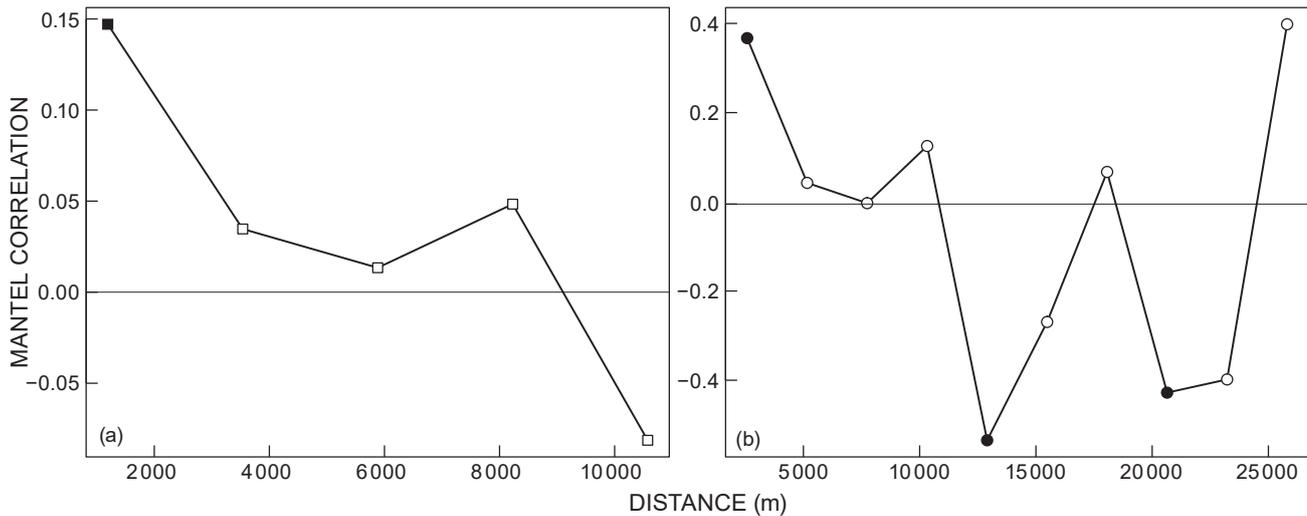


Figure 4: Mantel correlogram depicting spatial autocorrelation in macroinvertebrates, based on a Hellinger-transformed abundance data. (a) Results from simple Mantel tests, and (b) results from partial Mantel tests correcting for environmental differences. Filled circles indicate significant multivariate correlation calculated for each distance class

water by livestock and wildlife leading to cyanobacteria blooms (Hughes et al. 2016).

Impact of reserve protection on macroinvertebrate and large branchiopod community structure

Variation partitioning suggested that the unique effect of RP on macroinvertebrate community composition is rather small. However, 34 macroinvertebrate taxa were found exclusively in NGR, some of which are pollution sensitive (e.g. Elmidae, Hydraenidae and Naucoridae) (Day et al. 2002). In contrast, eight macroinvertebrate taxa were found exclusively in NCA, some of which can tolerate moderately to severely polluted waters (e.g. Ceratopogonidae, Gelastacoridae, Syrphidae and Tipulidae) (de Moor et al. 2003; Stals and de Moor 2007). Additionally, most common taxa from temporary pans (e.g. Dytiscidae, Corixidae and Notonectidae) occurred in both NGR and NCA. Similarly, our results also showed that RP had a significant effect on large branchiopod community composition by promoting gamma diversity rather than having pans with high species richness. In anthropogenically disturbed wetlands, species richness is usually one of the most affected community parameters (Trigal et al. 2007; Bouahim et al. 2014), especially for groups like large branchiopods that are highly dependent on temporary aquatic ecosystems (Nhiwatiwa et al. 2014). Large branchiopods may be used as a tool for indicating conservation status of pans in the study region, because in a similar study by Lumbreras et al. (2016), ponds with favourable conservation status also showed higher species richness of large branchiopods and other aquatic biota (e.g. plants and amphibians).

Our results also revealed that some of the variation in macroinvertebrate community composition was related to variation in local environmental conditions. Because environmental conditions in temporary wetlands tend to fluctuate, it is hard to identify consistent links between taxon composition and the environment (Schneider et al.

2015). Furthermore, long-term species composition of temporary wetlands connected to river systems is closely linked to habitat properties, such as river connectivity and their spatial location (Nhiwatiwa et al. 2011). To rule out the effects of river connectivity, the temporary pans that are directly connected to the river through channels and furrows were excluded in this study.

The spatial occurrence of macroinvertebrate communities at smaller spatial scales can be the result of nearby pans sharing specific environmental conditions (Langenheder and Ragnarsson 2007) or high dispersal rates especially for actively dispersing macroinvertebrates (Stoch et al. 2016). High dispersal rates among nearby pans can result in homogenisation of aquatic communities among close pans (Dube et al. 2017). Mantel analyses revealed significant spatial autocorrelation up to 2 km, corresponding to the scale at which dispersal is not limiting for some aquatic invertebrates in the studied region. When corrected for environmental differences, spatial autocorrelation was significant at various distances. At larger distances (>10 km), negative spatial autocorrelation was observed, which may indicate differences in environmental variables among pans. At the same time, dispersal may gradually become limiting at increasing spatial scales for some species, leading to increased dissimilarity among communities (Nhiwatiwa et al. 2011). To draw informed conclusions, replicated and time-integrating studies in similar habitat types are recommended (Bird and Day 2016).

Our results furthermore revealed a minor role of environmental factors and RP in shaping the macroinvertebrate and large branchiopod communities, as illustrated by the small proportion of community variation explained by these two factors. Also in several previous studies using variation partitioning to analyse macroinvertebrate and large branchiopod communities in temporary pools, a large proportion of the variation remained unexplained (Vanschoenwinkel et al. 2007;

Nhiwatiwa et al. 2011; Hill et al. 2017). The large amount of unexplained variation may firstly be caused by some unmeasured, but important variables for aquatic community composition in temporary aquatic habitats. For example, our study does not include additional factors known to be important determinants of community composition, such as hydroperiod (i.e. duration of aquatic phase) (Williams 2006). A positive association between hydroperiod and invertebrate richness and diversity was indeed shown in several studies (Waterkeyn et al. 2008; Nhiwatiwa et al. 2017), because the longer hydroperiod tends to provide more extensive opportunities for temporal niche segregation (Williams 2006). In systems with a short hydroperiod, failure of a population to complete the aquatic phase of their life cycle within a hydroperiod (e.g. large branchiopods), may result in a failure of the species to persist in that environment (Williams 2006). Second, our study is based on a single sampling event and does not capture temporal variation in community characteristics (Nhiwatiwa et al. 2011; Dube et al. 2017), which is often linked to temporal variation in environmental conditions (Torres et al. 2018). Third, environmental factors only explain a limited fraction of the variation in macroinvertebrate and large branchiopod communities, which could be as a result of stochasticity of community assembly, or importance of other meta-community dynamics (Jabot et al. 2019). Moreover, extremes in environmental variables are often associated with temporal variation and may have a significant effect on the community composition on the longer term (Williams 1996; Nhiwatiwa et al. 2011). Lastly, variation partitioning tends to undervalue the contribution explained by environmental variables (Gilbert and Bennett 2010), which might explain the low contribution of deterministic processes in shaping the macroinvertebrate and large branchiopod communities. Therefore, caution is needed when applying variation partitioning and interpreting the outcome. It should mainly be used as an exploratory tool together with other approaches. An assessment of 'hidden pond diversity' by hatching resting egg banks in the sediments under controlled environmental conditions (Brendonck and De Meester 2003) and relating it to soil abiotic variables, such as granulometry, chemical characteristics and dry organic matter content (Rogers 2014; Mabidi et al. 2016) could improve the resolution of studies of this nature. The water quality data are generally of limited use in species distribution patterns of 'hidden pond diversity', because of the fluctuation in physico-chemical parameters in temporary wetlands over a range of timescales (Rogers 2014).

Conclusions

Ndumo Game Reserve is a known biodiversity hotspot with protected status (Dube et al. 2015). Our study provides a first full assay of macroinvertebrate and large branchiopod diversity of temporary pans in NGR in comparison with the neighbouring communal land and provides a substantial argument for continued reserve protection. We show that protection of the pans by the reserve has an effect on the aquatic invertebrate community structure. Ndumo Game Reserve houses more taxa, particularly the flagship large branchiopod species, compared with the NCA. To

better understand the effect of reserve protection on the aquatic invertebrate diversity and community structure in the studied temporary pans, more frequent sampling and long-term sampling is required to capture seasonal dynamics. The temporary pans cannot be effectively conserved without a comprehensive understanding of their associated biodiversity. Therefore, the conservation of aquatic invertebrates in this region not only depends on the continued protection of the wetlands in NGR and NCA, but also on establishing continuous monitoring strategies.

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