



# Patterns in macroinvertebrate taxonomic richness and community assembly among urban wetlands in Cape Town, South Africa: implications for wetland management

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## Abstract

Urbanization has significantly increased globally during the last century and has far-reaching consequences for biodiversity and their associated habitats, particularly wetland ecosystems. Previous studies have focused primarily on wetlands in non-urban areas, and urban wetland biodiversity patterns are currently not well understood, particularly across Africa. Here, we investigate two highly transformed urban wetlands in Cape Town, South Africa, and determine the relative importance and influence of local environmental variables as drivers of macroinvertebrate richness and community structuring. We also determine the influence of local environmental variables for patterns of species turnover and nestedness within and among these wetlands, and provide management recommendations based on our findings. We found that few macroinvertebrate species were associated with these wetlands, yet community variation was driven by a combination of local environmental variables. Our results also indicate that the turnover component of beta diversity, rather than nestedness, was responsible for most of the variation in the overall macroinvertebrate community. We identified two major problems regarding the current ecological state of the investigated wetlands. Firstly, high nutrient loads originating from the surrounding land uses which reduced wetland biodiversity, and secondly, the transformation of these wetlands from seasonal to perennial water bodies. We recommend local and regional scale approaches to limit urban waste from entering these systems, and management of water levels simulating natural Mediterranean-type climate dynamics more closely are required to ensure that the maximum possible diversity can be supported in these wetlands.

**Keywords** Conservation · Diversity · Local environmental conditions · Nestedness · Pond · Turnover

## Introduction

Urbanization has significantly increased in proportion globally during the last century (Li et al. 2017), with urban settlements becoming more concentrated within cities and continuing to expand closer towards waterbodies, posing considerable risk to biodiversity (Reid et al. 2019). Increasing urban land cover has caused the fragmentation and loss of natural

habitat, degradation of remaining urban habitat, increased opportunities for the spread of alien invasive species, facilitated significant biological homogenization, and reduced local and regional species richness (Knop 2016). Urbanization can exert direct pressure on freshwater systems through infilling and draining, and indirectly through transformation of the surrounding terrestrial environment, hydrogeomorphological alterations, pollution from point and non-point sources (Camargo and Alonso 2006), and buildings and roads create physical barriers between remaining freshwater patches, reducing connectivity and opportunities for dispersal (McKinney 2008).

Inland wetlands are highly productive systems and have high social and economic value (Woodward and Wui 2001), providing important hydrological functions such as water purification, surface flow attenuation, and groundwater recharge (Zedler and Kercher 2005). Wetland systems also support a wide range of aquatic and terrestrial biotopes, and a high biodiversity of terrestrial (Parker et al. 2019) and aquatic (Moges

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et al. 2017; Hassall and Anderson 2015) flora and fauna. Despite their importance for ecology and society, about half of wetlands globally have been lost during the past century (Davidson 2014). Due to their small sizes relative to other freshwater systems, wetlands, especially in anthropogenically dominated landscapes, have received little research attention to date (Zacharias and Zamparas 2010). Wetlands have only recently been included in formal conservation efforts, following recognition of the threats facing these important habitats and the need protect the structure and function of remaining wetlands (Matthews 1993).

Local abiotic and biotic environmental variables have been previously demonstrated to be important determinants of wetland function and biodiversity (Thornhill et al. 2018). In particular, changes in vegetation complexity and alteration of flow characteristics have been reported to influence wetland function and species composition (Batzer et al. 2006). Changes to water chemistry, especially related to water temperature, pH, salinity levels, dissolved oxygen concentration and nutrient loads are also important drivers of wetland biodiversity (Carrino-Kyker and Swanson 2007). Despite this, few attempts have been made to explore the relationships between landscape transformation (particularly the conversion of natural land to urban development), environmental conditions and wetland biodiversity (Carrino-Kyker and Swanson 2007).

As is the case in other regions globally, past and present landcover transformation poses a great risk to seasonal and perennial wetlands in South Africa, which are now among the most threatened ecosystems in the country (Mlambo et al. 2011). Before the urban development of the Cape Town Metropolitan area, this landscape was rich in seasonal and perennial wetlands, varying in size and ecological function (Day 1987). Since the rapid expansion of the human population and the associated urban sprawl, it is estimated that more than 97% of all wetlands have already been lost, primarily through draining and infilling (Cowan 1995). Other impacts such as nutrient enrichment have led to the degradation in wetland quality and function, and biodiversity losses in the remaining wetlands, especially those in close association with urban settlements (Davies and Day 1998).

Given their uncertain fate globally (Davidson 2014), there has been increasing recognition that wetlands, including the few remaining in urban areas such as the Cape Town Metropolitan area, require urgent rehabilitation and management intervention to prevent further biodiversity losses (Day 1987). Reducing non-climate impacts, alien invasive species control, strategic selection and management of restoration areas, raising awareness of wetland losses in the public and private sectors, and long-term monitoring are among the proposed conservation measures to mitigate further wetland losses (Erwin 2009). Due to the urgency of wetland conservation, rapid but effective assessment tools are required, spanning multiple disciplines (Hassall 2014) to support the intended measures.

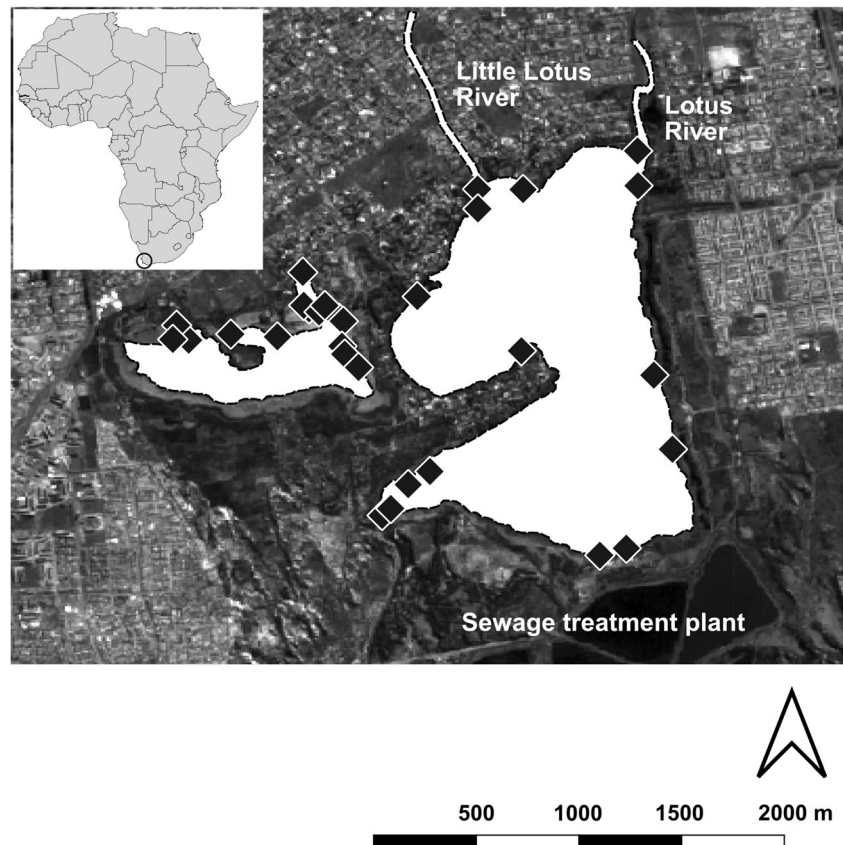
Despite the paucity of research and threats facing wetland ecology, there is now growing interest globally in determining the local environmental factors that influence species richness and composition of aquatic macroinvertebrates occupying lentic habitats in urban environments globally (Hassall 2014; Hill et al. 2017b). As yet, we have limited understanding of local factors driving species richness and assembly within and among urban wetlands (Batzer et al. 2006). Aquatic macroinvertebrates greatly contribute to overall wetland biodiversity, possess a range of ecological adaptations enabling their rapid responses to changes in their environments and are relatively easy to sample (Batzer 2013). Aquatic macroinvertebrate alpha and beta diversity patterns in relation to environmental gradients may reveal important factors regarding changes in ecological state of freshwater habitats and provide critical information for conservation and management decisions involving wetlands impacted by urban development. Here, we determine the relative importance and influence of local environmental variables as drivers of aquatic macroinvertebrate species richness and community structure (total beta-diversity, turnover and nestedness) within and among two adjacent urban wetlands in Cape Town, South Africa. We also provide management recommendations to improve the ecological resilience and biodiversity levels of urban wetlands.

## Materials and methods

### Study sites

The city of Cape Town falls within the Mediterranean-type Cape Floristic Region (CFR) biodiversity hotspot and covers about 400 km<sup>2</sup>, with a population of 4.62 million people. Two adjacent wetlands in the south of Cape Town (Zeekoevlei and Rondevlei) were selected for study (Fig. 1). Zeekoevlei is among one of the most recently proclaimed conservation areas in Cape Town, being the largest of all remaining surface waterbodies located on the Cape Flats (about 2.6 km<sup>2</sup> in size) with an average depth of 2 m throughout (Harding and Wright 1999). Zeekoevlei is fed by the Lotus and Little Lotus Rivers originating from the north, draining a catchment of roughly 80 km<sup>2</sup>. Urban development and market gardening activities dominate the northern and eastern surroundings of the Zeekoevlei catchment area while the southern side is adjacent to the Cape Flats sewage treatment plant. Surrounded by urban land use, Rondevlei lies to the west of Zeekoevlei and is approximately 0.5 km<sup>2</sup> in size (Fig. 1). Rondevlei has no surface connection with Zeekoevlei, after the channel connecting these two wetlands was closed in the 1950s (Harding and Wright 1999). Rondevlei is proclaimed a formal nature reserve where large populations of several aquatic avian species feed, rest and breed. Historically, both wetlands were intermittent with highly variable hydrology, often drying

**Fig. 1** Map of study area and significant landscape features. Black diamonds indicate sampling localities



during low precipitation seasons and re-wetting during high precipitation seasons (Harding and Wright 1999). Both have been transformed from intermittent to perennial wetlands since the construction of respective weirs in the early 1900s, and water level fluctuation has since been anthropogenically managed. Both are surrounded almost entirely by *Typha capensis* (Rohrb.) N.E.Br., *Phragmites australis* (Cav.) Steud. and *Schoenoplectus* sp., serving as nesting sites for many avian species.

### Macroinvertebrate sampling

Field sampling was from the end of June to mid-July 2019. The sampling period represented the winter rainfall season of the CFR, when water levels of both wetlands were highest. Most focal macroinvertebrates are also present as aquatic immature stages during the rain season, while adult Coleoptera are highly abundant in the region during this time. The sampling period further represented the recovery season after 'drawdown', the period at the end of April each year when outflow is artificially initiated, so allowing for nutrient rich water to exit the system. Aquatic macroinvertebrates with body sizes  $>0.5$  cm were sampled using a standard pond net (300 mm  $\times$  300 mm, 1000  $\mu$ m mesh size). Branchiopoda was also included, as they are considered effective indicators water toxicity levels (Yuan et al. 2017). Fifteen random quadrats of

25 m<sup>2</sup> were selected along the margin of each wetland (30 quadrats in total; Fig. 1), and were chosen to represent all mesohabitats present (i.e. submerged macrophytes, emergent macrophytes and open water). Each quadrat was sampled for three minutes, dividing sampling time proportionally among mesohabitats to best reflect dominant mesohabitats (Biggs et al. 1998). Netted samples were transferred to resealable storage bags and preserved in 70% ethanol. All macroinvertebrate fauna were sorted, counted and identified to at least genus level, although some Diptera larvae could only be resolved to family level. Identification was aided by the South African Water Research Commission field guides (Barber-James and Lugo-Ortiz 2003; Harrison 2003; Reavell 2003; Stals 2003) as well as some other published resources (Suhling et al. 2014; Griffiths et al. 2015; Seaman et al. 1999).

### Environmental data collection

At each quadrat, a range of physical, chemical and biological variables were measured in situ. Physical and chemical variables included: average depth (cm), conductivity ( $\mu$ S cm<sup>-1</sup>), pH, water temperature ( $^{\circ}$ C), estimated water clarity (clear vs. turbid as categorical variable), substrate composition (% clay/silt content, % sand content, % decomposing organic material), and estimated visual pollution levels (scale of 1–10, maximum value being heavily polluted). Biological variables

included: % emergent vegetation cover, % submerged vegetation cover, and presence/absence of non-native vegetation. In addition, one water sample for each quadrat was collected and tested remotely for arsenic (As), cadmium (Cd), chlorine (Cl), chromium (Cr), mercury (Hg), lead (Pb), nitrate-nitrogen (NO<sub>3</sub>-N), nitrite-nitrogen (NO<sub>2</sub>-N), phosphate (PO<sub>4</sub>) and dissolve oxygen (O<sub>2</sub>) concentration levels (mg/L), as well as *Escherichia coli* Migula 1895 levels (cfu/100 ml), and fecal coliform levels (cfu/100 ml).

## Statistical analysis

All statistical analyses involving biological data were performed in the R environment (R development Core Team 2016). To determine macroinvertebrate sampling adequacy, we constructed species accumulation curves for observed species richness across all sampling sites, as well as species richness for Zeekoevlei and Rondevlei separately, using the *vegan* package (Oksanen et al. 2017). The Chao2 species richness estimator, and the Incidence-based Coverage Estimator (ICE) were calculated to estimate the number of species that remained undiscovered overall, as well as within each wetland, using the *fossil* package (Vavrek 2011).

Overall species richness, as well as species richness for Zeekoevlei and Rondevlei individually, were normally distributed according to Shapiro-Wilks tests for normality, and Mantel test showed no spatial autocorrelation among sampling localities (Online Resource 1). We used linear modelling to determine the effects of local environmental variables on overall species richness, and species richness for Zeekoevlei and Rondevlei separately, using the *lme4* package for R (Bates et al. 2014). Spearman's rank order correlation tests were used to determine covariation among the recorded environmental variables, using the *pairs.panels* function in the *psych* package (Revelle 2019; Online Resource 2). Where variables were strongly correlated, only one in the pair was included in further analysis. After these considerations, eleven variables were included for linear modelling. These were: % emergent vegetation cover, % submerged vegetation cover, conductivity, pH, temperature, dissolved oxygen, Cl, PO<sub>4</sub>, NO<sub>2</sub>-N, fecal coliform levels (positively covariate with *E. coli* levels), and percentage clay substrate composition (negatively covariate with percentage sandy substrate composition).

To determine the order of magnitude in which local environmental variables influenced our three species richness sets, we performed model selection and averaging using the *MuMIn* package (Barton 2019). For the three species richness sets, we used second-order Akaike's information criterion (AIC<sub>C</sub>) values to rank all candidate models, and  $\Delta$ AIC<sub>C</sub> values to determine whether more than one model was important. Best model subsets were those where the explanatory models had  $\Delta$ AIC<sub>C</sub> values  $\leq 2$ . We then performed model averaging over the subsets of best models for our species

richness sets. For each model averaging scenario, 95% confidence interval values are reported, and environmental variables were considered significant when confidence intervals did not include 0. Unconditional estimated values were used to determine the direction of relationships among species richness and significant environmental variables.

Total beta diversity of the overall macroinvertebrate community, as well as the separate communities of Zeekoevlei and Rondevlei, was represented by the Jaccard dissimilarity measure (based on presence/absence macroinvertebrate data). Total beta diversity was partitioned into species turnover (the replacement of species among sampling localities; Baselga 2010) and nestedness (i.e. differences in taxonomic richness among sampling sites; Viana et al. 2016) components using the *beta.multi* function in the *betapart* package (Baselga et al. 2017). Pair-wise distance matrices accounting for total beta diversity, the turnover component and the nestedness component of beta diversity were calculated for the overall macroinvertebrate community, as well as for the separate communities of Zeekoevlei and Rondevlei, using the *beta.pair* function. For each distance matrix, principle coordinate analysis (PCoA) with Lingoes corrections (Legendre 2014) was used to obtain corrected eigenvectors using the *ape* package (Paradis and Schliep 2018). Local environmental variables were Log<sub>10</sub> transformed to eliminate their physical units (Legendre and Birks 2012).

Obtained PCoA eigenvectors were used as input response variables, and Log<sub>10</sub>-transformed environmental variables as predictors. Redundancy analysis (RDA) employing a forward selection procedure was performed using the *ordi2step* function in the *vegan* package to identify the significant environmental drivers of total beta diversity, and the turnover and nestedness components of beta diversity, for the total macroinvertebrate community, and the separate communities of Zeekoevlei and Rondevlei. Partial RDA analyses were employed to determine the relative contribution of local environmental variables to overall variation in total beta diversity, and the turnover and nestedness components of beta diversity for the overall macroinvertebrate community, and the separate macroinvertebrate communities.

Inverse distance weighting (IDW) spatial interpolation was performed in QGIS (Quantum GIS Development Team 2017) to transform point data to raster data and produce a 10 m spatial resolution visualization of overall gradients in significant local environmental conditions among the fifteen sampling localities for Zeekoevlei and Rondevlei. Since the weight of predicted values increases as distance decreases between sampling localities (Elumalai et al. 2017), spatial interpolation was performed separately for each wetland to eliminate the effects of sampling localities within one wetland that were in close proximity to sampling localities in the other. For all interpolations, a distance coefficient equal to two was used. Although a broad estimation, IDW interpolation works

well in the absence of dense sampling localities and does not estimate values that are higher than observed input values, providing a great advantage over other interpolation or extrapolation methods (Czajkowski et al. 2017).

## Results

### Relative effects of local environmental variables on alpha diversity, total beta diversity, turnover and nestedness

A total of 29,872 macroinvertebrate individuals and 22 species from 18 families were sampled (see Online Resource 3 for full species list). The total number of species sampled, as well as the number of species sampled for Zeekoevlei (17 species) and Rondevlei (16 species) individually, neared the estimated number of species (Chao2 and Incidence-based Coverage Estimator (ICE); Table 1), indicating that data collected were representative. All but two sampled macroinvertebrates (*Tomichia ventricosa* Reeve 1842 and one unidentified *Tomichia* freshwater snail species) were common and widespread species. Both species occupied Zeekoevlei, but only *T. ventricosa* was recorded from Rondevlei.

Of the eleven local environmental variables considered, model selection identified six as important for driving variation in species richness. These were: percentage emergent vegetation cover, conductivity, dissolved oxygen, pH, temperature, and NO<sub>2</sub>-N concentration (Table 2). Although percentage emergent vegetation cover, conductivity, dissolved oxygen and pH were selected as important drivers of overall species richness, model averaging results indicated that none of these selected variables had significant effects on overall species richness. No local environmental variables were selected as important drivers of species richness for Zeekoevlei. For Rondevlei, conductivity, NO<sub>2</sub>-N concentration, pH and temperature were selected as important drivers of species richness. Model averaging results showed that species richness decreased significantly with increasing conductivity, increasing NO<sub>2</sub>-N concentration, increasing pH, and increasing temperature.

**Table 1** Individual abundance, number of observed species (Sobs), and Chao2 and Incidence-based Coverage (ICE) estimators for sampling effort overall, and within the two adjacent wetlands

	Abundance	Sobs	Chao2	ICE
Overall	29,872	22	25.6	23.7
Zeekoevlei	3399	17	19.5	18.9
Rondevlei	26,473	16	18.0	17.5

The overall macroinvertebrate community showed high levels of total beta diversity (Jaccard dissimilarity = 0.9478). Variation in the overall community could mostly be explained by the turnover component of beta diversity (partial Jaccard dissimilarity = 0.9021 (95.2% contribution)), rather than the nestedness component of beta diversity (partial Jaccard dissimilarity = 0.0456 (4.8% contribution)). For total beta diversity, forward selection identified three significant local variables, explaining a total of 79% of variation in community composition (Fig. 2a). These were: percentage submerged vegetation cover, conductivity, and dissolved oxygen. Percentage submerged vegetation cover explained 5.9% of variation in total beta diversity, dissolved oxygen explained 7.1% of variation, and conductivity explained 10.3% of variation. Dissolved oxygen and conductivity combined explained 10.8% of variation in total beta diversity, dissolved oxygen and percentage submerged vegetation cover combined explained 12.9% of variation, and percentage submerged vegetation cover and conductivity combined explained 15.4% of variation. All three selected variables combined explained 16.2% of variation in total beta diversity.

For the turnover component of total beta diversity, forward selection identified two significant local variables, explaining a total of 6% of variation in community composition (Fig. 2b). These were percentage submerged vegetation cover and NO<sub>2</sub>-N concentration. Percentage submerged vegetation cover explained 1.3% of variation, while NO<sub>2</sub>-N concentration explained 1.4% of variation in overall turnover. Percentage submerged vegetation cover and NO<sub>2</sub>-N concentration combined explained 2.9% of variation in overall turnover. No significant local variables were selected for the nestedness component of beta diversity.

The separate macroinvertebrate communities of Zeekoevlei and Rondevlei showed lower levels of total beta diversity compared to the overall macroinvertebrate community, yet remained high (Jaccard dissimilarity = 0.8857 and 0.9098 respectively). Variation in Zeekoevlei and Rondevlei communities was mostly explained by the turnover component of beta diversity (Zeekoevlei partial Jaccard dissimilarity = 0.8025 (90.6% contribution); Rondevlei partial Jaccard dissimilarity = 0.8063 (88.6% contribution)), rather than the nestedness component of beta diversity (Zeekoevlei partial Jaccard dissimilarity = 0.0832 (9.4% contribution); Rondevlei partial Jaccard dissimilarity = 0.1034 (11.4% contribution)). For Zeekoevlei, no significant local variables were selected for total beta diversity, the turnover component of beta diversity, nor the nestedness component of beta diversity. For Rondevlei, forward selection identified percentage submerged vegetation cover as a significant local variable for total beta diversity and the turnover component of beta diversity, explaining 12.9% of variation in total beta diversity, and 6.5% of variation in the turnover component of beta diversity respectively.

**Table 2** Model averaged estimates of local variables driving variation in overall species richness, and species richness within each wetland separately

Selected variables	Estimate	SE	95% CI	Relative importance	Number of containing models
<i>Overall</i>					
% Emergent vegetation cover	0.0209	0.0170	-0.0126, 0.0543	0.2880	2
Conductivity	-0.0007	0.0006	-0.0019, 0.0005	0.2670	2
Dissolved oxygen	-0.0743	0.0656	-0.2029, 0.0543	0.1720	1
pH	0.5062	0.7226	-0.9100, 1.9225	0.1070	1
<i>Zeekoevlei</i>					
No selected variables	N/A	N/A	N/A	N/A	N/A
<i>Rondevlei</i>					
Conductivity	<b>-0.0020</b>	<b>0.0006</b>	<b>-0.0033, -0.0008</b>	<b>0.5900</b>	<b>1</b>
Nitrite	<b>-193.9110</b>	<b>65.6108</b>	<b>-322.5059, -65.3161</b>	<b>0.5900</b>	<b>1</b>
pH	<b>-6.8909</b>	<b>2.9356</b>	<b>-12.6446, -1.1371</b>	<b>0.5900</b>	<b>1</b>
Temperature	<b>-1.8841</b>	<b>0.5639</b>	<b>-2.9894, -0.7788</b>	<b>0.5900</b>	<b>1</b>

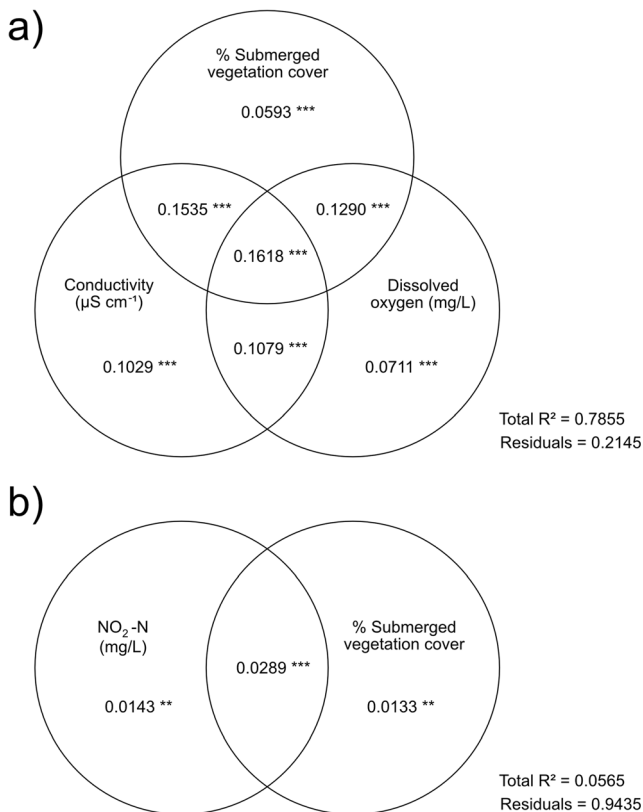
Relative importance indicates the sum of Akaike weights over all models in the best model subset (models with  $\Delta AICC \leq 2$ , under each modelling scenario), in which the variable was included. Number of containing models indicate the number of times the variable was selected as important in the best model subset. Significant traits (95% CI of the estimates does not cross the 0 threshold) are highlighted in bold text

### Environmental gradients of Zeekoevlei and Rondevlei

Overall, Rondevlei had higher % submerged vegetation cover than Zeekoevlei, and was highest along the northern (85%

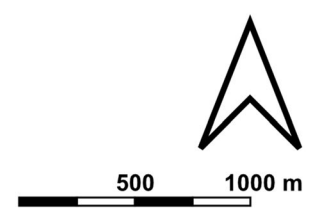
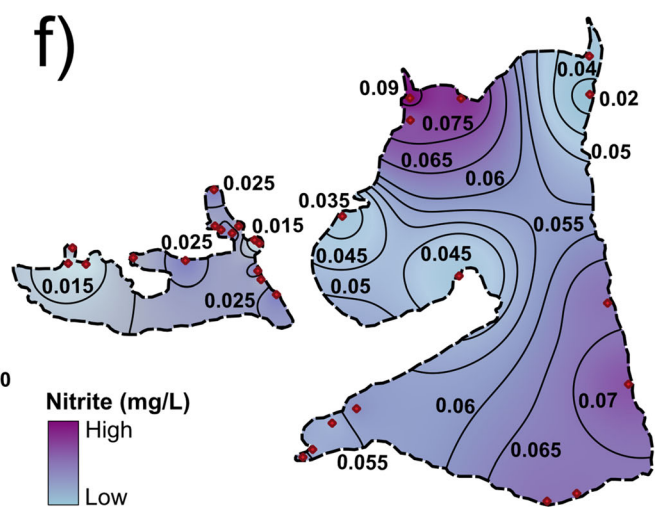
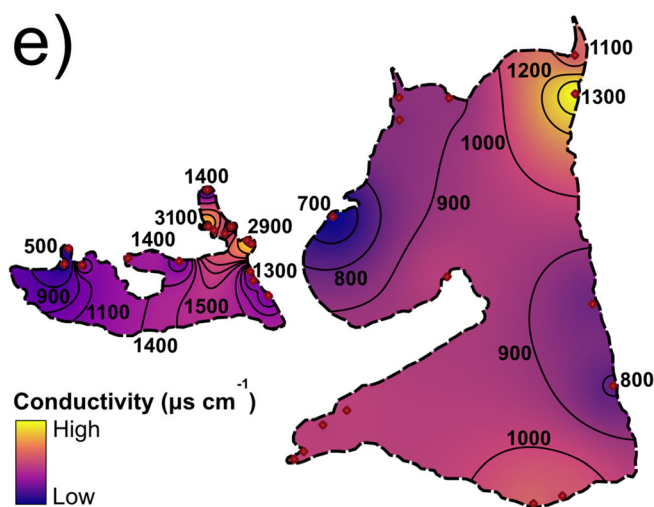
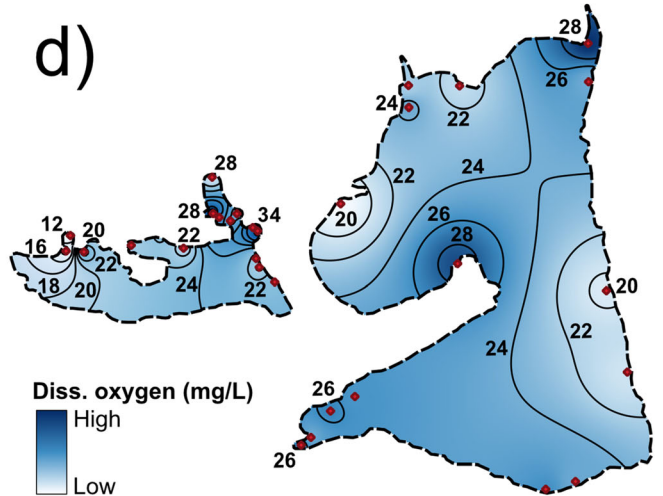
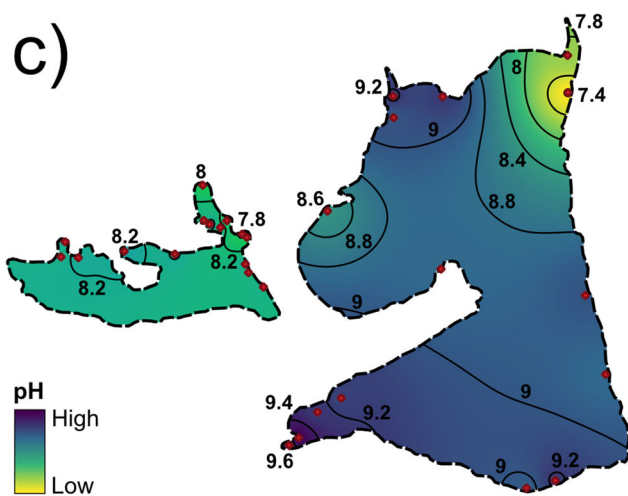
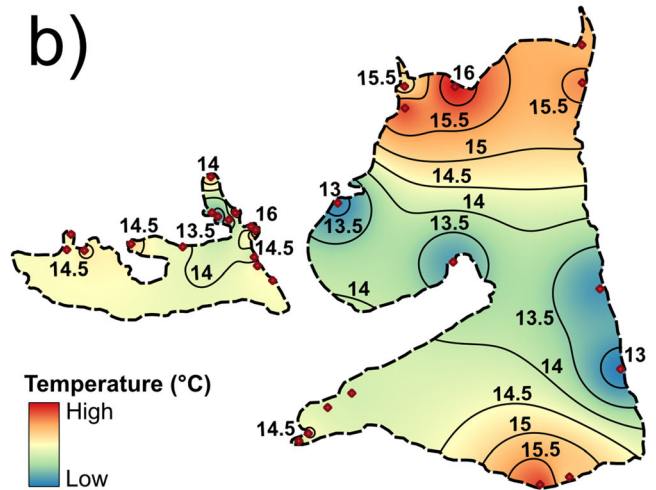
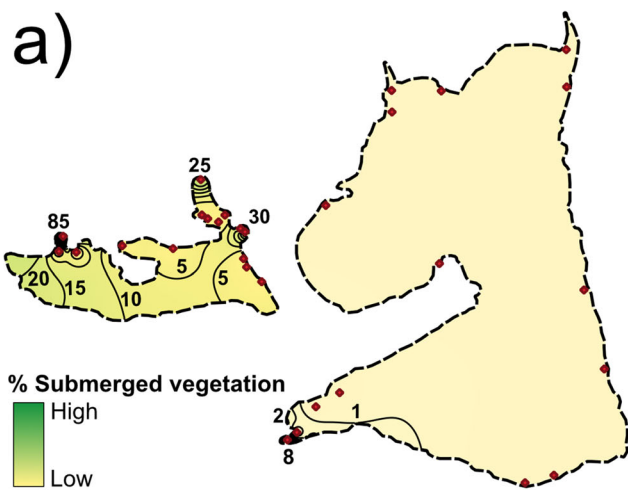
cover) and western margins (ranging between 25% and 30% cover) of Rondevlei (Fig. 3a). Zeekoevlei had almost no submerged vegetation, except for limited cover around the outlet in the south-western corner (8% cover). Rondevlei had more constant water temperature throughout compared to Zeekoevlei, with water temperature mostly ranging from  $\sim 14$  °C to 14.5 °C and reaching 16 °C along the shallow eastern margin (Fig. 3b). Zeekoevlei had higher water temperatures along the northern margin (15.5 °C to 16 °C) as well as the shallow southern margin (15.5 °C), but had lower water temperature along the eastern and western margins, as well as the central region (13 °C to 13.5 °C). pH was also more constant for Rondevlei compared to Zeekoevlei, ranging between 7.8 and 8.2 (Fig. 3c). For Zeekoevlei, pH ranged between 8.6 and 9 throughout, but was lower along the north-eastern margin (ranging between 7.4 and 7.8) and higher around the outlet in the south-western corner (9.4 to 9.6).

Dissolved oxygen concentration was more variable for Rondevlei compared to Zeekoevlei, and ranged between 12 mg/L along the north-western margin to 34 mg/L along the eastern margin (Fig. 3d). For Zeekoevlei, dissolved oxygen concentration was highest along the central region and the Lotus River inlet (28 mg/L), and was lowest along the western and eastern margins (20 mg/L). Conductivity was relatively more constant for Zeekoevlei, ranging between 800  $\mu\text{S cm}^{-1}$  and 1000  $\mu\text{S cm}^{-1}$  throughout (Fig. 3e), with the exception of one locality along the western margin (700  $\mu\text{S cm}^{-1}$ ), and one



**Fig. 2** Relative contribution of local environmental variables to variation in (a) overall macroinvertebrate total beta diversity and (b) the turnover component of beta diversity. Values indicate adjusted R<sup>2</sup> values. Significance levels: \*\*:  $p < 0.01$ ; \*\*\*:  $p < 0.001$

**Fig. 3** Interpolated gradients of (a) % submerged vegetation cover, (b) water temperature, (c) pH, (d) dissolved oxygen concentration, (e) conductivity, and (f) nitrite concentration for Zeekoevlei and Rondevlei at 10 m spatial resolution. Red circles indicate sampling localities



along the eastern margin ( $1300 \mu\text{S cm}^{-1}$ ). For Rondevlei, conductivity mostly ranged between  $900 \mu\text{S cm}^{-1}$  and  $1500 \mu\text{S cm}^{-1}$ , but dropped to  $500 \mu\text{S cm}^{-1}$  in along the north-western margin and increased to  $3100 \mu\text{S cm}^{-1}$  along the north-eastern margin. Finally,  $\text{NO}_2\text{-N}$  concentration was more constant for Rondevlei compared to Zeekoevlei, and ranged between  $0.015 \text{ mg/L}$  and  $0.025 \text{ mg/L}$  throughout (Fig. 3f).  $\text{NO}_2\text{-N}$  concentration for Zeekoevlei was overall higher than for Rondevlei, and was highest around the Little Lotus River inlet in the northwest ( $0.09 \text{ mg/L}$ ) and the south-eastern margin ( $0.07 \text{ mg/L}$ ).  $\text{NO}_2\text{-N}$  concentration was lowest around the Lotus River inlet ( $0.02 \text{ mg/L}$ ) and the western margin ( $0.035 \text{ mg/L}$ ).

## Discussion

Despite the wetlands being in the CFR biodiversity hotspot, species richness and endemism were much lower for the studied urban wetlands than would be expected for the region (Mlambo et al. 2011; Bird and Day 2016). This indicates that urban development in close proximity to wetland ecosystems can significantly reduce their environmental and ecological conditions (Heino et al. 2017). Species richness and overall macroinvertebrate community varied among wetlands and was driven by a concert of local environmental variables. The turnover component of beta diversity, rather than nestedness, explained the majority of overall community variation. High species turnover and the overall importance of local environmental conditions indicate that species replacement through niche occupancy was an important driver of aquatic macroinvertebrate community variation, even at the scale of individual wetlands (Viana et al. 2016). However, variation in the importance of local environmental variables for structuring species richness gradients and beta diversity in individual wetlands indicates that wetland context is important, and should be reflected in management and conservation practices.

### Relationships between alpha diversity, beta diversity, and local environmental variables

Our results provide little evidence that high macroinvertebrate species richness is associated with relatively high levels of % submerged vegetation cover, at least for the generalist species sampled here. Other studies on lentic systems in the region (Deacon et al. 2019), and elsewhere in South Africa (Briggs et al. 2019) indicated that high insect species richness is often associated with intermediate levels of % submerged vegetation cover, since vegetation provides a range of microhabitats to breed and feed (Fairchild et al. 2003). Excessive vegetation cover can lead to reduced species occupancy, through the accumulation of organic debris, which in turn

creates high loads of decaying organic matter and unstable dissolved oxygen levels (Mnaya et al. 2006). We found that the presence and abundance of submerged vegetation drives macroinvertebrate community variation and species replacement, even at the scale of a single wetland, since some macroinvertebrates require water that is free from dense vegetation that causes shading (Briggs et al. 2019). Vertebrate and invertebrate predators are also associated with vegetation, and some small macroinvertebrates absent from submerged vegetation may be free-living in open water to avoid predation (Courtney and Cranston 2015). We found no significant role of marginal vegetation as a driver of macroinvertebrate species richness or community variation. The lack of influence of marginal vegetation is likely related to cover being limited to single species (here, *T. capensis*, *P. australis* or *Schoenoplectus* sp.), so limiting vegetation complexity and the availability of resources.

Water chemistry components have previously been reported as important drivers of aquatic macroinvertebrate species richness and community variation in lentic systems at regional (Hill et al. 2017a) and local scales (Biggs et al. 2005). Our results indicate that dissolved oxygen concentration was a significant driver of overall community variation, which likely reflects the dependence on dissolved oxygen for respiration by aquatic macroinvertebrates. However, we found some macroinvertebrates that are atmospheric breathers (e.g. hemipterans; Lytle 2015), or have other respiratory adaptations (e.g. most larval dipterans; Courtney and Cranston 2015) enabling them to occupy areas with low dissolved oxygen and free of larger predatory species which require higher levels of dissolved oxygen, such as dragonfly larvae (Suhling et al. 2015). These findings were further supported by lower species richness being associated with relatively higher water temperature in our results, since high water temperature is often associated with low dissolved oxygen content. Warmer water may also increase vertebrate and invertebrate predator activity, especially in the case of large species which do not rely on dissolved oxygen for respiration, such as actively hunting dytiscid beetles and/or ambush predatory corixids (Lytle 2015; Yee and Kehl 2015).

Low species richness was associated with relatively higher  $\text{NO}_2\text{-N}$  concentrations, and variation in  $\text{NO}_2\text{-N}$  concentration levels also led to higher levels of species replacement. Although limited empirical evidence is available, nitrite toxicity inhibits the respiratory function of some freshwater species (Camargo and Alonso 2006) and insects are in general more sensitive to high levels of nitrite in freshwater compared to crustaceans and mollusks (Soucek and Dickinson 2012). Given the overall high concentration levels of  $\text{NO}_2\text{-N}$  pollution in the wetlands investigated here, especially for Zeekoevlei, pollution sensitive macroinvertebrates are likely excluded completely from these wetland systems while more opportunities are created for generalist species, so driving



species turnover. Our evidence for species richness decreasing with increasing water pH supports previous hypotheses for the metabolic inhibitory influence of elevated nitrite concentrations, as higher NO<sub>2</sub>-N concentrations are associated with higher water pH (Camargo and Alonso 2006). Water characterized by pH deviating from neutral were also occupied by generalist species (e.g. *Dicrotendipes pilosimanus* Kieffer 1914, *Marsupiobdella africana* Goddard & Malan 1913), likely with wider tolerance ranges compared to specialists, supporting findings for other lentic insect groups occupying natural ponds and artificial reservoirs in the region (Deacon et al. 2019). We also found that steep gradients in conductivity levels (as a proxy for salinity) influenced overall macroinvertebrate community variation, and lower species richness was associated with high conductivity levels. As with high NO<sub>2</sub>-N concentration and pH, high conductivity levels interfere with the metabolic function and water retention capabilities of freshwater macroinvertebrates (James et al. 2003), shaping local and regional aquatic assemblages.

### Implications for management

Our results indicate that both wetlands supported a limited macroinvertebrate biodiversity and that physicochemical heterogeneity drove overall richness and turnover of those species (Viana et al. 2016). Habitat heterogeneity, even for generalist taxa at the scale of individual wetlands, is a strong driving force of aquatic macroinvertebrate occupancy, generating gradients of environmental conditions suitable for a range of macroinvertebrates with variable habitat requirements (Tessier et al. 2004). These findings were further supported by the overall high importance of community turnover in our models. Maintaining habitat heterogeneity at regional scales, especially those components related to vegetation complexity and water chemistry, may be most effective to ensure broad environmental gradients are maintained (Thomaz and Ribeiro de Cunha 2010). However, given the variation in local environmental variables among the studied urban wetlands, additional management strategies should be focused at the scale of individual (local) wetlands to ensure that the site-specific context of wetlands is accounted for. In doing so, conservation actions can be maximized to mitigate the effects of landcover transformation on these highly threatened ecosystems (Mlambo et al. 2011).

Detailed empirical data are superficial or lacking for the region in most cases, challenging our ability to comment on the past ecological importance of these wetlands. Due to safety concerns, the small wetlands in the area surrounding Zeekoevlei and Rondevlei which are overall exempt from human disturbance are extremely difficult to access, further challenging our ability to place the investigated wetlands in the regional context. Nevertheless, we identify two major problems regarding the current ecological state of these two

wetlands. The first is the high nutrient loads originating from the surrounding land uses which eliminate wetland biodiversity. High levels of inorganic nitrogen enter freshwater through urban and agricultural runoff, industrial waste and sewage effluent, leading to elevated algal growth (Camargo et al. 2005). These biodiversity declines can also have adverse effects on human health (Camargo and Alonso 2006). The conversion of inorganic nitrogen to organic forms also consumes dissolved oxygen, leading to highly anoxic water conditions and unstable water temperature (Camargo and Alonso 2006). Here, we recorded highest concentrations of inorganic nitrogen at wetland inlets and along the southern margin of Zeekoevlei, adjacent to a sewage treatment plant. This indicates that measures to prevent urban waste from entering these wetlands should take priority. This would require a regional water quality management approach, encompassing the entire catchment area, and tackling the source of the pollution from the inlet rivers.

The second major problem is the transformation of these wetlands from historical intermittence associated with the Mediterranean-type climate to perennial water bodies. We found no ecologically sensitive macroinvertebrate species, although some occupy smaller and less hydrologically impacted seasonal wetlands in the region (Mlambo et al. 2011; Bird and Day 2016), or have historically been recorded from the investigated wetlands (e.g. *Pseudagrion draconis* Barnard 1937; Samways and Simaika 2016). Vegetation heterogeneity and complexity associated with the naturally dynamic state have been reduced, and this reduction is likely to have contributed to these wetlands being unattractive habitats for specialist species which require temporally complex habitats to persist (Williams 2006). By anthropogenically maintaining a permanent hydrology, natural cycles of filling and flushing during wet seasons and drying during dry seasons are restricted, leading to accumulation of inorganic nitrogen and consequently, eutrophication. Allowing regular inflow and outflow to and from these wetlands would periodically reduce algal growth to restore clearer water. Consequently, submerged macrophyte growth would be encouraged, extensive cover by alien marginal vegetation would be controlled without using harmful herbicides, and biodiversity recovery would be stimulated over time (Moges et al. 2017). However, abrupt changes in water level could lead to nuisance species (e.g. *D. pilosimanus* and *M. africana*) population explosions. We thus recommend that water level fluctuation is managed to simulate natural dynamics more closely, through gradual changes in water level spanning dry seasons, when seasonal declining water levels would have occurred naturally. We acknowledge that implementation of these management recommendations can be challenging and requires commitment and collaboration among regional and local conservation authorities, and all other stakeholders along with support from the public.

The low importance of macroinvertebrate community nestedness in our models indicates that the nearly complete hydrological isolation of the wetlands through urbanization and associated wetland loss has likely limited colonization by taxa from the few surrounding wetlands that remain on the Cape Flats, irrespective of the current detrimental environmental conditions. As a result, only passively dispersing taxa which are able to tolerate these adverse environmental conditions are able to persist in the two investigated wetlands in their current environmental state. For actively dispersing taxa which are theoretically able to travel over extended distances to seek favorable habitats, low quality wetlands may act as ecological traps, where taxa are able to reach these wetlands, but are not able to persist (Deacon et al. 2019). Consequently, low water quality creates a niche vacuum for highly tolerant taxa, many of which are nuisance species. Due to safety and accessibility limitations, we were unable to investigate the effects of spatial context among multiple wetlands in the catchment, but we expect that wetland connectivity is an important driver of macroinvertebrate colonization and occupancy, as has been demonstrated for urban ponds in the UK (Hill et al. 2017a). Yet, the relatively narrow spatial scale of our investigation allowed us to observe clearer relationships between anthropogenically-induced changes to habitat quality and macroinvertebrate diversity patterns (Bird and Day 2016).

In conclusion, biological communities associated with wetlands respond to changes in their habitats, and ongoing urban development pose a risk to biodiversity through modification of chemical gradients and vegetation at both local and regional scale. These changes lead to a reduction in habitat complexity and increases in pollution, which in turn eliminate sensitive species, but likely create a niche vacuum for species which are less sensitive. Management measures can be taken to reduce the impact of urban development on urban wetland systems. Although complete restoration is unrealistic, implementing mitigation measures can greatly improve ecological conditions in urban wetlands so that they resemble their former, natural state. Rehabilitating wetlands through mitigating pollution levels and encouraging natural flow dynamics improves ecological function and provides aquatic taxa with refuge habitats during a time of unprecedented global land use change.

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## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflicts of interest.

**Ethics approval** Not applicable.

**Consent to participate** Not applicable.

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