

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

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5 Charl Deacon<sup>1\*</sup>, Bethany R. S. Fox<sup>2</sup>, Leigh Morland<sup>2</sup>, Michael J. Samways<sup>1</sup>, Shannon  
6 Weaver<sup>3</sup>, Ruth Massey<sup>2</sup> and Matthew J. Hill<sup>2</sup>

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9 <sup>1</sup>Department of Conservation Ecology and Entomology, Stellenbosch University, Matieland,  
10 South Africa.

11  
12 <sup>2</sup>School of Applied Sciences, University of Huddersfield, Queensgate, Huddersfield, HD1  
13 3DH, UK.

14  
15 <sup>3</sup>University of Cape Town, Rondebosch, Cape Town, 7700, South Africa.

16  
17  
18 **\* Author for correspondence**

19 Charl Deacon  
20 Room 3014  
21 Department of Conservation Ecology and Entomology (JS Marais Building)  
22 Stellenbosch University  
23 Stellenbosch  
24 South Africa  
25 charldeacon@sun.ac.za  
26 (+27) 83 275 9298

27  
28  
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34 **Abstract**

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

55 **Keywords** Conservation, diversity, local environmental conditions, nestedness, pond,  
56 turnover.

57

## 58 **Introduction**

59 Urbanization has significantly increased in proportion globally during the last century (Li et al.  
60 2017), with urban settlements becoming more concentrated within cities and continuing to  
61 expand closer towards waterbodies, posing considerable risk to biodiversity (Reid et al. 2019).  
62 Increasing urban land cover has caused the fragmentation and loss of natural habitat,  
63 degradation of remaining urban habitat, increased opportunities for the spread of alien invasive  
64 species, facilitated significant biological homogenization, and reduced local and regional  
65 species richness (Knop 2016). Urbanization can exert direct pressure on freshwater systems  
66 through infilling and draining, and indirectly through transformation of the surrounding  
67 terrestrial environment, hydrogeomorphological alterations, pollution from point and non-  
68 point sources (Camargo & Alonso 2006), and buildings and roads create physical barriers  
69 between remaining freshwater patches, reducing connectivity and opportunities for dispersal  
70 (McKinney 2008).

71

72 Inland wetlands are highly productive systems and have high social and economic value  
73 (Woodward & Wui 2001), providing important hydrological functions such as water  
74 purification, surface flow attenuation, and groundwater recharge (Zedler & Kercher 2005).  
75 Wetland systems also support a wide range of aquatic and terrestrial biotopes, and a high  
76 biodiversity of terrestrial (Parker et al. 2019) and aquatic (Moges et al. 2017; Hassall &  
77 Anderson 2015) flora and fauna. Despite their importance for ecology and society, about half  
78 of wetlands globally have been lost during the past century (Davidson 2014). Due to their small  
79 sizes relative to other freshwater systems, wetlands, especially in anthropogenically dominated  
80 landscapes, have received little research attention to date (Zacharias & Zamparas 2010).  
81 Wetlands have only recently been included in formal conservation efforts, following

82 recognition of the threats facing these important habitats and the need protect the structure and  
83 function of remaining wetlands (Matthews 1993).

84

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

95

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

106

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

116

117 Given the paucity of research and threats facing wetland ecology, there has been growing  
118 interest globally in determining the local environmental factors that influence species richness  
119 and composition of aquatic macroinvertebrates occupying lentic habitats in urban  
120 environments globally (Hassall 2014; Hill et al. 2017b). As yet, we have limited understanding  
121 of local factors driving species richness and assembly within and among urban wetlands  
122 (Batzer et al. 2006). Aquatic macroinvertebrates greatly contribute to overall wetland  
123 biodiversity, possess a range of ecological adaptations enabling their rapid responses to  
124 changes in their environments and are relatively easy to sample (Batzer 2013). Aquatic  
125 macroinvertebrate alpha and beta diversity patterns in relation to environmental gradients may  
126 reveal important factors regarding changes in ecological state of freshwater habitats and  
127 provide critical information for conservation and management decisions involving wetlands  
128 impacted by urban development. Here, we determine the relative importance and influence of  
129 local environmental variables as drivers of aquatic macroinvertebrate species richness and  
130 community structure (total beta-diversity, turnover and nestedness) within and among two

131 adjacent urban wetlands in Cape Town, South Africa. We also provide management  
132 recommendations to improve the ecological resilience and biodiversity of urban wetlands.

133

## 134 **Materials and methods**

### 135 *Study sites*

136 The city of Cape Town falls within the Mediterranean-type Cape Floristic Region (CFR)  
137 biodiversity hotspot and covers about 400 km<sup>2</sup>, with a population of 4.62 million people. Two  
138 adjacent wetlands in the south of Cape Town (Zeekoevlei and Rondevlei) were selected for  
139 study (Fig. 1). Zeekoevlei is among one of the most recently proclaimed conservation areas in  
140 Cape Town, being the largest of all remaining surface waterbodies located on the Cape Flats  
141 (about 2.6 km<sup>2</sup> in size) with an average depth of 2 m throughout (Harding et al. 1999).  
142 Zeekoevlei is fed by the Lotus and Little Lotus Rivers originating from the north, draining a  
143 catchment of roughly 80 km<sup>2</sup>. Urban development and market gardening activities dominate  
144 the northern and eastern surroundings of the Zeekoevlei catchment area while the southern side  
145 is adjacent to the Cape Flats sewage treatment plant. Surrounded by urban land use, Rondevlei  
146 lies to the west of Zeekoevlei and is approximately 0.5 km<sup>2</sup> in size (Fig. 1). Rondevlei has no  
147 surface connection with Zeekoevlei, after the channel connecting these two wetlands was  
148 closed in the 1950s (Harding et al. 1999). Rondevlei is proclaimed a formal nature reserve  
149 where large populations of several aquatic avian species feed, rest and breed. Historically, both  
150 wetlands were intermittent with highly variable hydrology, often drying during low  
151 precipitation seasons and re-wetting during high precipitation seasons (Harding et al. 1999).  
152 Both have been transformed from intermittent to perennial wetlands since the construction of  
153 respective weirs in the early 1900s, and water level fluctuation has since been  
154 anthropogenically managed. Both are surrounded almost entirely by *Typha capensis* (Rohrb.)

155 N.E.Br., *Phragmites australis* (Cav.) Steud. and *Schoenoplectus* sp., serving as nesting sites  
156 for many avian species.

### 157 ***Macroinvertebrate sampling***

158 Field sampling was from the end of June to mid-July 2019. The sampling period represented  
159 the winter rainfall season of the CFR, when water levels of both wetlands were highest. Most  
160 focal macroinvertebrates are also present as aquatic immature stages during the rain season,  
161 while adult Coleoptera are highly abundant in the region during this time. The sampling period  
162 further represented the recovery season after ‘drawdown’, the period at the end of April each  
163 year when outflow is artificially initiated, so allowing for nutrient rich water to exit the system.  
164 Aquatic macroinvertebrates with body sizes > 0.5 cm were sampled using a standard pond net  
165 (300 mm x 300 mm, 1000 µm mesh size). Branchiopoda was also included, as they are  
166 considered effective indicators water toxicity levels (Yuan et al. 2017). Fifteen random  
167 quadrats of 25 m<sup>2</sup> were selected along the margin of each wetland (30 quadrats in total; Fig.  
168 1), and were chosen to represent all mesohabitats present (i.e. submerged macrophytes,  
169 emergent macrophytes and open water). Each quadrat was sampled for three minutes, dividing  
170 sampling time proportionally among mesohabitats to best reflect dominant mesohabitats  
171 (Biggs et al. 1998). Netted samples were transferred to resealable storage bags and preserved  
172 in 70 % ethanol. All macroinvertebrate fauna were sorted, counted and identified to at least  
173 genus level, although some Diptera larvae could only be resolved to family level. Identification  
174 was aided by the South African Water Research Commission field guides (Barber-James &  
175 Lugo-Ortiz 2003; Harrison 2003; Reavell 2003; Stals 2003) as well as some other published  
176 resources (Suhling et al. 2014; Griffiths et al. 2015; Seaman et al. 1999).

177

### 178 ***Environmental data collection***

179 At each quadrat, a range of physical, chemical and biological variables were measured *in situ*.  
180 Physical and chemical variables included: average depth (cm), conductivity ( $\mu\text{S cm}^{-1}$ ), pH,  
181 water temperature ( $^{\circ}\text{C}$ ), estimated water clarity (clear vs. turbid as categorical variable),  
182 substrate composition (% clay/silt content, % sand content, % decomposing organic material),  
183 and estimated visual pollution levels (scale of 1-10, maximum value being heavily polluted).  
184 Biological variables included: % emergent vegetation cover, % submerged vegetation cover,  
185 and presence/absence of non-native vegetation. In addition, one water sample for each quadrat  
186 was collected and tested remotely for arsenic (As), cadmium (Cd), chlorine (Cl), chromium  
187 (Cr), mercury (Hg), lead (Pb), nitrate-nitrogen ( $\text{NO}_3\text{-N}$ ), nitrite-nitrogen ( $\text{NO}_2\text{-N}$ ), phosphate  
188 ( $\text{PO}_4$ ) and dissolve oxygen ( $\text{O}_2$ ) concentration levels (mg/L), as well as *Escherichia coli* Migula  
189 1895 levels (cfu/100 ml), and fecal coliform levels (cfu/100 ml).

190

### 191 ***Statistical analysis***

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

199

200 Overall species richness, as well as species richness for Zeekoevlei and Rondevlei individually,  
201 were normally distributed according to Shapiro-Wilks tests for normality, and Mantel test  
202 showed no spatial autocorrelation among sampling localities (Online Resource 1). We used



203 linear modelling to determine the effects of local environmental variables on overall species  
204 richness, and species richness for Zeekoevlei and Rondevlei separately, using the *lme4* package  
205 for R (Bates et al. 2014). Spearman's rank order correlation tests were used to determine  
206 covariation among the recorded environmental variables, using the *pairs.panels* function in the  
207 *psych* package (Revelle 2019; Online Resource 2). Where variables were strongly correlated,  
208 only one in the pair was included in further analysis. After these considerations, eleven  
209 variables were included for linear modelling. These were: % emergent vegetation cover, %  
210 submerged vegetation cover, conductivity, pH, temperature, dissolved oxygen, Cl, PO<sub>4</sub>, NO<sub>2</sub>-  
211 N, fecal coliform levels (positively covariate with *E. coli* levels), and percentage clay substrate  
212 composition (negatively covariate with percentage sandy substrate composition).

213

214 To determine the order of magnitude in which local environmental variables influenced our  
215 three species richness sets, we performed model selection and averaging using the *MuMIn*  
216 package (Barton 2019). For the three species richness sets, we used second-order Akaike's  
217 information criterion (AIC<sub>C</sub>) values to rank all candidate models, and  $\Delta$ AIC<sub>C</sub> values to  
218 determine whether more than one model was important. Best model subsets were those where  
219 the explanatory models had  $\Delta$ AIC<sub>C</sub> values  $\leq 2$ . We then performed model averaging over the  
220 subsets of best models for our species richness sets. For each model averaging scenario, 95%  
221 confidence interval values are reported, and environmental variables were considered  
222 significant when confidence intervals did not include 0. Unconditional estimated values were  
223 used to determine the direction of relationships among species richness and significant  
224 environmental variables.

225

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

239

240 Obtained PCoA eigenvectors were used as input response variables, and  $\text{Log}_{10}$ -transformed  
241 environmental variables as predictors. Redundancy analysis (RDA) employing a forward  
242 selection procedure was performed using the *ordi2step* function in the *vegan* package to  
243 identify the significant environmental drivers of total beta diversity, and the turnover and  
244 nestedness components of beta diversity, for the total macroinvertebrate community, and the  
245 separate communities of Zeekoevlei and Rondevlei. Partial RDA analyses were employed to  
246 determine the relative contribution of local environmental variables to overall variation in total  
247 beta diversity, and the turnover and nestedness components of beta diversity for the overall  
248 macroinvertebrate community, and the separate macroinvertebrate communities.

249

250 Inverse distance weighting (IDW) spatial interpolation was performed in QGIS (Quantum GIS  
251 Development Team 2017) to transform point data to raster data and produce a 10 m spatial  
252 resolution visualization of overall gradients in significant local environmental conditions  
253 among the fifteen sampling localities for Zeekoevlei and Rondevlei. Since the weight of  
254 predicted values increases as distance decreases between sampling localities (Elumalai et al.  
255 2017), spatial interpolation was performed separately for each wetland to eliminate the effects  
256 of sampling localities within one wetland that were in close proximity to sampling localities in  
257 the other. For all interpolations, a distance coefficient equal to two was used. Although a broad  
258 estimation, IDW interpolation works well in the absence of dense sampling localities and does  
259 not estimate values that are higher than observed input values, providing a great advantage over  
260 other interpolation or extrapolation methods (Czajkowski et al. 2017).

261

## 262 **Results**

### 263 *Relative effects of local environmental variables on alpha diversity, total beta diversity,* 264 *turnover and nestedness*

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

273

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

285

286 The overall macroinvertebrate community showed high levels of total beta diversity (Jaccard  
287 dissimilarity = 0.9478). Variation in the overall community could mostly be explained by the  
288 turnover component of beta diversity (partial Jaccard dissimilarity = 0.9021 (95.2 %  
289 contribution)), rather than the nestedness component of beta diversity (partial Jaccard  
290 dissimilarity = 0.0456 (4.8 % contribution)). For total beta diversity, forward selection  
291 identified three significant local variables, explaining a total of 79% of variation in community  
292 composition (Fig. 2a). These were: percentage submerged vegetation cover, conductivity, and  
293 dissolved oxygen. Percentage submerged vegetation cover explained 5.9 % of variation in total  
294 beta diversity, dissolved oxygen explained 7.1 % of variation, and conductivity explained 10.3  
295 % of variation. Dissolved oxygen and conductivity combined explained 10.8 % of variation in  
296 total beta diversity, dissolved oxygen and percentage submerged vegetation cover combined  
297 explained 12.9 % of variation, and percentage submerged vegetation cover and conductivity

298 combined explained 15.4 % of variation. All three selected variables combined explained 16.2  
299 % of variation in total beta diversity.

300

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

308

309 The separate macroinvertebrate communities of Zeekoevlei and Rondevlei showed lower  
310 levels of total beta diversity compared to the overall macroinvertebrate community, yet  
311 remained high (Jaccard dissimilarity = 0.8857 and 0.9098 respectively). Variation in  
312 Zeekoevlei and Rondevlei communities was mostly explained by the turnover component of  
313 beta diversity (Zeekoevlei partial Jaccard dissimilarity = 0.8025 (90.6 % contribution);  
314 Rondevlei partial Jaccard dissimilarity = 0.8063 (88.6 % contribution)), rather than the  
315 nestedness component of beta diversity (Zeekoevlei partial Jaccard dissimilarity = 0.0832 (9.4  
316 % contribution); Rondevlei partial Jaccard dissimilarity = 0.1034 (11.4 % contribution)). For  
317 Zeekoevlei, no significant local variables were selected for total beta diversity, the turnover  
318 component of beta diversity, nor the nestedness component of beta diversity. For Rondevlei,  
319 forward selection identified percentage submerged vegetation cover as a significant local  
320 variable for total beta diversity and the turnover component of beta diversity, explaining 12.9

321 % of variation in total beta diversity, and 6.5 % of variation in the turnover component of beta  
322 diversity respectively.

323

### 324 *Environmental gradients of Zeekoevlei and Rondevlei*

325 Overall, Rondevlei had higher % submerged vegetation cover than Zeekoevlei, and was highest  
326 along the northern (85% cover) and western margins (ranging between 25% and 30% cover)  
327 of Rondevlei (Fig 3a). Zeekoevlei had almost no submerged vegetation, except for limited  
328 cover around the outlet in the south-western corner (8% cover). Rondevlei had more constant  
329 water temperature throughout compared to Zeekoevlei, with water temperature mostly ranging  
330 from ~14 °C to 14.5 °C and reaching 16 °C along the shallow eastern margin (Fig 3b).  
331 Zeekoevlei had higher water temperatures along the northern margin (15.5 °C to 16 °C) as well  
332 as the shallow southern margin (15.5 °C), but had lower water temperature along the eastern  
333 and western margins, as well as the central region (13 °C to 13.5 °C). pH was also more  
334 constant for Rondevlei compared to Zeekoevlei, ranging between 7.8 and 8.2 (Fig 3c). For  
335 Zeekoevlei, pH ranged between 8.6 and 9 throughout, but was lower along the north-eastern  
336 margin (ranging between 7.4 and 7.8) and higher around the outlet in the south-western corner  
337 (9.4 to 9.6).

338

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

345 margin ( $700 \mu\text{S cm}^{-1}$ ), and one along the eastern margin ( $1300 \mu\text{S cm}^{-1}$ ). For Rondevlei,  
346 conductivity mostly ranged between  $900 \mu\text{S cm}^{-1}$  and  $1500 \mu\text{S cm}^{-1}$ , but dropped to  $500 \mu\text{S}$   
347  $\text{cm}^{-1}$  in along the north-western margin and increased to  $3100 \mu\text{S cm}^{-1}$  along the north-eastern  
348 margin. Finally,  $\text{NO}_2\text{-N}$  concentration was more constant for Rondevlei compared to  
349 Zeekoevlei, and ranged between  $0.015 \text{ mg/L}$  and  $0.025 \text{ mg/L}$  throughout (Fig 3f).  $\text{NO}_2\text{-N}$   
350 concentration for Zeekoevlei was overall higher than for Rondevlei, and was highest around  
351 the Little Lotus River inlet in the northwest ( $0.09 \text{ mg/L}$ ) and the south-eastern margin ( $0.07$   
352  $\text{mg/L}$ ).  $\text{NO}_2\text{-N}$  concentration was lowest around the Lotus River inlet ( $0.02 \text{ mg/L}$ ) and the  
353 western margin ( $0.035 \text{ mg/L}$ ).

354

## 355 **Discussion**

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

370

371 ***Relationships between alpha diversity, beta diversity, and local environmental variables***

372 Our results provide little evidence that high macroinvertebrate species richness is associated  
373 with relatively high levels of % submerged vegetation cover, at least for the generalist species  
374 sampled here. Other studies on lentic systems in the region (Deacon et al. 2019), and elsewhere  
375 in South Africa (Briggs et al. 2019) indicated that high insect species richness is often  
376 associated with intermediate levels of % submerged vegetation cover, since vegetation  
377 provides a range of microhabitats to breed and feed (Fairchild et al. 2003). Excessive vegetation  
378 cover can lead to reduced species occupancy, through the accumulation of organic debris,  
379 which in turn creates high loads of decaying organic matter and unstable dissolved oxygen  
380 levels (Mnaya et al. 2006). We found that the presence and abundance of submerged vegetation  
381 drives macroinvertebrate community variation and species replacement, even at the scale of a  
382 single wetland, since some macroinvertebrates require water that is free from dense vegetation  
383 that causes shading (Briggs et al. 2019). Vertebrate and invertebrate predators are also  
384 associated with vegetation, and some small macroinvertebrates absent from submerged  
385 vegetation may be free-living in open water to avoid predation (Courtney & Cranston 2015).  
386 We found no significant role of marginal vegetation as a driver of macroinvertebrate species  
387 richness or community variation. The lack of influence of marginal vegetation is likely related  
388 to cover being limited to single species (here, *T. capensis*, *P. australis* or *Schoenoplectus* sp.),  
389 so limiting vegetation complexity and the availability of resources.

390

391 Water chemistry components have previously been reported as important drivers of aquatic  
392 macroinvertebrate species richness and community variation in lentic systems at regional (Hill  
393 et al. 2017a) and local scales (Biggs et al. 2005). Our results indicate that dissolved oxygen  
394 concentration was a significant driver of overall community variation, which likely reflects the



395 dependence on dissolved oxygen for respiration by aquatic macroinvertebrates. However, we  
396 found some macroinvertebrates that are atmospheric breathers (e.g. hemipterans; Lytle 2015),  
397 or have other respiratory adaptations (e.g. most larval dipterans; Courtney & Cranston 2015)  
398 enabling them to occupy areas with low dissolved oxygen and free of larger predatory species  
399 which require higher levels of dissolved oxygen, such as dragonfly larvae (Suhling et al. 2015).  
400 These findings were further supported by lower species richness being associated with  
401 relatively higher water temperature in our results, since high water temperature is often  
402 associated with low dissolved oxygen content. Warmer water may also increase vertebrate and  
403 invertebrate predator activity, especially in the case of large species which do not rely on  
404 dissolved oxygen for respiration, such as actively hunting dytiscid beetles and/or ambush  
405 predatory corixids (Lytle 2015; Yee & Kehl 2015).

406

407 Low species richness was associated with relatively higher NO<sub>2</sub>-N concentrations, and  
408 variation in NO<sub>2</sub>-N concentration levels also led to higher levels of species replacement.  
409 Although limited empirical evidence is available, nitrite toxicity inhibits the respiratory  
410 function of some freshwater species (Camargo & Alonso 2006) and insects are in general more  
411 sensitive to high levels of nitrite in freshwater compared to crustaceans and mollusks (Soucek  
412 & Dickinson 2012). Given the overall high concentration levels of NO<sub>2</sub>-N pollution in the  
413 wetlands investigated here, especially for Zeekoevlei, pollution sensitive macroinvertebrates  
414 are likely excluded completely from these wetland systems while more opportunities are  
415 created for generalist species, so driving species turnover. Our evidence for species richness  
416 decreasing with increasing water pH supports previous hypotheses for the metabolic inhibitory  
417 influence of elevated nitrite concentrations, as higher NO<sub>2</sub>-N concentrations are associated with  
418 higher water pH (Camargo & Alonso 2006). Water characterized by pH deviating from neutral  
419 were also occupied by generalist species (e.g. *Dicrotendipes pilosimanus* Kieffer 1914,

420 *Marsupiobdella Africana* Goddard & Malan 1913), likely with wider tolerance ranges  
421 compared to specialists, supporting findings for other lentic insect groups occupying natural  
422 ponds and artificial reservoirs in the region (Deacon et al. 2019). We also found that steep  
423 gradients in conductivity levels (as a proxy for salinity) influenced overall macroinvertebrate  
424 community variation, and lower species richness was associated with high conductivity levels.  
425 As with high NO<sub>2</sub>-N concentration and pH, high conductivity levels interfere with the  
426 metabolic function and water retention capabilities of freshwater macroinvertebrates (James et  
427 al. 2003), shaping local and regional aquatic assemblages.

428

#### 429 ***Implications for management***

430 Our results indicate that both wetlands supported a limited macroinvertebrate biodiversity and  
431 that physicochemical heterogeneity drove overall richness and turnover of those species (Viana  
432 et al. 2016). Habitat heterogeneity, even for generalist taxa at the scale of individual wetlands,  
433 is a strong driving force of aquatic macroinvertebrate occupancy, generating gradients of  
434 environmental conditions suitable for a range of macroinvertebrates with variable habitat  
435 requirements (Tessier et al. 2004). These findings were further supported by the overall high  
436 importance of community turnover in our models. Maintaining habitat heterogeneity at  
437 regional scales, especially those components related to vegetation complexity and water  
438 chemistry, may be most effective to ensure broad environmental gradients are maintained  
439 (Thomaz & Ribeiro de Cunha 2010). However, given the variation in local environmental  
440 variables among the studied urban wetlands, additional management strategies should be  
441 focused at the scale of individual (local) wetlands to ensure that the site-specific context of  
442 wetlands is accounted for. In doing so, conservation actions can be maximized to mitigate the  
443 effects of landcover transformation on these highly threatened ecosystems (Mlambo et al.  
444 2011).

445

446 Detailed empirical data are superficial or lacking for the region in most cases, challenging our  
447 ability to comment on the past ecological importance of these wetlands. Due to safety concerns,  
448 the small wetlands in the area surrounding Zeekoevlei and Rondevlei which are overall exempt  
449 from human disturbance are extremely difficult to access, further challenging our ability to  
450 place the investigated wetlands in the regional context. Nevertheless, we identify two major  
451 problems regarding the current ecological state of these two wetlands. The first is the high  
452 nutrient loads originating from the surrounding land uses which eliminate wetland biodiversity.  
453 High levels of inorganic nitrogen enter freshwater through urban and agricultural runoff,  
454 industrial waste and sewage effluent, leading to elevated algal growth (Camargo et al. 2005).  
455 These biodiversity declines can also have adverse effects on human health (Camargo & Alonso  
456 2006). The conversion of inorganic nitrogen to organic forms also consumes dissolved oxygen,  
457 leading to highly anoxic water conditions and unstable water temperature (Camargo & Alonso  
458 2006). Here, we recorded highest concentrations of inorganic nitrogen at wetland inlets and  
459 along the southern margin of Zeekoevlei, adjacent to a sewage treatment plant. This indicates  
460 that measures to prevent urban waste from entering these wetlands should take priority. This  
461 would require a regional water quality management approach, encompassing the entire  
462 catchment area, and tackling the source of the pollution from the inlet rivers.

463

464 The second major problem is the transformation of these wetlands from historical intermittence  
465 associated with the Mediterranean-type climate to perennial water bodies. We found no  
466 ecologically sensitive macroinvertebrate species, although some occupy smaller and less  
467 hydrologically impacted seasonal wetlands in the region (Mlambo et al. 2011; Bird & Day  
468 2016), or have historically been recorded from the investigated wetlands (e.g. *Proischnura*  
469 *subfurcata* Ris 1921; Samways & Simaika 2016). Vegetation heterogeneity and complexity

470 associated with the naturally dynamic state have been reduced, and this reduction is likely to  
471 have contributed to these wetlands being unattractive habitats for specialist species which  
472 require temporally complex habitats to persist (Williams 2006). By anthropogenically  
473 maintaining a permanent hydrology, natural cycles of filling and flushing during wet seasons  
474 and drying during dry seasons are restricted, leading to accumulation of inorganic nitrogen and  
475 consequently, eutrophication. Allowing regular inflow and outflow to and from these wetlands  
476 would periodically reduce algal growth to restore clearer water. Consequently, submerged  
477 macrophyte growth would be encouraged, extensive cover by alien marginal vegetation would  
478 be controlled without using harmful herbicides, and biodiversity recovery would be stimulated  
479 over time (Moges et al. 2017). However, abrupt changes in water level could lead to nuisance  
480 species (e.g. *D. pilosimanus* and *M. africana*) population explosions. We thus recommend that  
481 water level fluctuation is managed to simulate natural dynamics more closely, through gradual  
482 changes in water level spanning dry seasons, when seasonal declining water levels would have  
483 occurred naturally. We acknowledge that implementation of these management  
484 recommendations can be challenging and requires commitment and collaboration among  
485 regional and local conservation authorities, and all other stakeholders along with support from  
486 the public.

487

488 The low importance of macroinvertebrate community nestedness in our models indicates that  
489 the nearly complete hydrological isolation of the wetlands through urbanization and associated  
490 wetland loss has likely limited colonization by taxa from the few surrounding wetlands that  
491 remain on the Cape Flats, irrespective of the current detrimental environmental conditions. As  
492 a result, only passively dispersing taxa which are able to tolerate these adverse environmental  
493 conditions are able to persist in the two investigated wetlands in their current environmental  
494 state. For actively dispersing taxa which are theoretically able to travel over extended distances

495 to seek favorable habitats, low quality wetlands may act as ecological traps, where taxa are  
496 able to reach these wetlands, but are not able to persist (Deacon et al. 2019). Consequently,  
497 low water quality creates a niche vacuum for highly tolerant taxa, many of which are nuisance  
498 species. Due to safety and accessibility limitations, we were unable to investigate the effects  
499 of spatial context among multiple wetlands in the catchment, but we expect that wetland  
500 connectivity is an important driver of macroinvertebrate colonization and occupancy, as has  
501 been demonstrated for urban ponds in the UK (Hill et al. 2017a). Yet, the relatively narrow  
502 spatial scale of our investigation allowed us to observe clearer relationships between  
503 anthropogenically-induced changes to habitat quality and macroinvertebrate diversity patterns  
504 (Bird & Day 2016).

505

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

517

518 **Declarations**

519 ***Funding***

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521 ***Conflicts of interest***

522 The authors declare that they have no conflicts of interest.

523 ***Ethics approval***

524 Not applicable

525 ***Consent to participate***

526 Not applicable

527 ***Consent for publication***

528 Not applicable

529 ***Availability of data and material***

530 All data relevant to this study are available at [10.6084/m9.figshare.12609032](https://doi.org/10.6084/m9.figshare.12609032).

531 ***Code availability***

532 All data relevant to this study are available at [10.6084/m9.figshare.12609032](https://doi.org/10.6084/m9.figshare.12609032).

533 ***Authors' contributions***

534 **Charl Deacon:** Conceptualization, Methodology, Formal analysis, Investigation, Data  
535 curation, Writing – Original draft, Visualization, Resources, Project administration.

536 **Bethany R. S. Fox:** Writing – Review and editing, Project administration, Funding  
537 acquisition.

538 **Leigh Morland:** Writing – Review and editing, Project administration, Funding acquisition.

539 **Michael J. Samways:** Resources, Writing – Review and editing.

540 **Shannon Weaver:** Writing – Review and editing.

- 541 **Ruth Massey:** Writing – Review and editing, Funding acquisition.
- 542 **Matthew J. Hill:** Conceptualization, Methodology, Formal analysis, Investigation, Data
- 543 curation, Writing – Review and editing, Project administration, Funding acquisition.

544 **References**

545 Barber-James HM, Lugo-Ortiz CR. 2003. Ephemeroptera. In: de Moor I, Day J, de Moor F,  
546 editors. *Guides to the Freshwater invertebrates of Southern Africa: Insecta I Ephemeroptera,*  
547 *Odonata and Plecoptera.* Water Research Commission, Pretoria, South Africa. pp. 16-142.

548

549 Barton K. 2019. MuMIn: Multi-model inference. R package version 1.42.1. Retrieved from  
550 <https://CRAN.R-project.org/package=MuMIn>.

551

552 Baselga A, Orme D, Villeger S, De Bortoli J, Leprieur F. 2017. Betapart: Partitioning beta  
553 diversity into turnover and nestedness components. R package version 1.3. Retrieved from  
554 <https://CRAN.R-project.org/package=betapart>.

555

556 Baselga A. 2010. Partitioning the turnover and nestedness components of beta diversity.  
557 *Global Ecology and Biogeography* 19: 134-143.

558

559 Bates D, Maechler M, Bolker B, Walker S. 2014. lme4: Linear mixed-effects models using  
560 S4 classes. R package version 1.1-7. Retrieved from [https://CRAN.R-project.](https://CRAN.R-project.org/package=lme4)  
561 [org/package=lme4](https://CRAN.R-project.org/package=lme4).

562

563 Batzer DP. 2013. The seemingly intractable ecological responses of invertebrates in North  
564 American wetlands: a review. *Wetlands* 33: 1-15.

565

566 Batzer DP, Cooper R, Wissinger SA. 2006. Wetland animal ecology. Pages 242-284 in:

567 Batzer DP, Sharitz RR, editors. *Ecology of freshwater and estuarine wetlands.* University of  
568 California Press, Berkeley.



569

570 Biggs J, Fox G, Nicolet P, Walker D, Whitfield M, Williams P. 1998. A guide to the methods  
571 of the National Pond Survey. Pond Action, Oxford.

572

573 Biggs J, Williams P, Whitfield M, Nicolet P, Weatherby A. 2005. 15 years of pond  
574 assessment in Britain: results and lessons learned from the work of Pond  
575 Conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems* 15: 693-714.

576

577 Bird MS, Day JA. 2016. Impacts of terrestrial habitat transformation on temporary wetland  
578 invertebrates in a sclerophyllous sand fynbos landscape. *Hydrobiologia* 782: 169-185.

579

580 Briggs AJ, Pryke JS, Samways MJ, Conlong DE. 2019. Macrophytes promote aquatic insect  
581 conservation in artificial ponds. *Aquatic Conservation: Marine and Freshwater Ecosystems* 29:  
582 1190-1201.

583

584 Camargo JA, Alonso A. 2006. Ecological and toxicological effects of inorganic nitrogen  
585 pollution in aquatic ecosystems: a global assessment. *Environment International* 32: 831-849.

586

587 Camargo JA, Alonso A, Salamanca A. 2005. Nitrate toxicity to aquatic animals: a review  
588 with new data for freshwater invertebrates. *Chemosphere* 58: 1255-1267.

589

590 Carrino-Kyker SR, Swanson AK. 2007. Seasonal physicochemical characteristics of thirty  
591 Northern Ohio temporary pools along gradients of GIS-delineated human land-use. *Wetlands*  
592 27: 749-760.

593

594 Courtney GW, Cranston PS. 2015. Chapter 40: Order Diptera. Pages 2155-2182 in Thorp JH,  
595 Rogers DC, editors. Thorp and Covich's freshwater invertebrates: Ecology and general  
596 biology. Elsevier, Amsterdam.  
597

598 Cowan GI. 1995. Wetland Regions of South Africa. Department of Environmental Affairs  
599 and Tourism, Pretoria.  
600

601 Czajkowski J, Villarini G, Montgomery M, Michel-Kerjan E, Goska R. 2017. Assessing  
602 current and future freshwater flood risk from North Atlantic tropical cyclones via insurance  
603 claims. *Nature* 7: 41609.  
604

605 Davidson N. 2014. How much wetland has the world lost? Long-term and recent trends in  
606 global wetland area. *Marine Freshwater Research* 65: 934-942.  
607

608 Davies BR, Day JA. 1998. *Vanishing Waters*. University of Cape Town Press, Cape Town.  
609

610 Day JA. 1987. Conservation and management of wetlands in the greater Cape Town area. In:  
611 Walmesley RD, Botten ML, compilers. *Proceedings of a Symposium on Ecology and*  
612 *Conservation of Wetlands in South Africa*. Occasional Report Series No 28. Ecosystem  
613 Programmes. Foundation for Research Development, CSIR, Pretoria.  
614

615 Deacon C, Samways MJ, Pryke JS. 2019. Aquatic insects decline in abundance and occupy  
616 low-quality artificial habitats to survive hydrological droughts. *Freshwater Biology* 64: 1643-  
617 1654.  
618

619 Elumalai V, Brindha K, Sithole B, Lakshmanan E. 2017. Spatial interpolation methods and  
620 geostatistics for mapping groundwater contamination in a coastal area. *Environmental*  
621 *Science and Pollution Research*, 24: 11601-11617.

622

623 Erwin KL. 2009. Wetlands and global climate change: the role of wetland restoration in a  
624 changing world. *Wetlands Ecology and Management* 17: 71-84.

625

626 Fairchild GW, Cruz J, Faulds M, Short AEZ, Matta JF. 2003. Microhabitat and landscape  
627 influences on aquatic beetle assemblages in a cluster of temporary and permanent ponds.  
628 *Journal of the North American Benthological Society* 22: 224-240.

629

630 Griffiths C, Day J, Picker M. 2015. *Freshwater Life. A field guide to the plants and animals*  
631 *of southern Africa*. Struik Nature, Cape Town, South Africa.

632

633 Harding WR, Wright S. 1999. Initial findings regarding changes in phyto- and zooplankton  
634 composition and abundance following the temporary drawdown and refilling of a shallow,  
635 hypertrophic South African coastal lake. *Journal of Lake and Reservoir Management* 15: 47-  
636 53.

637

638 Harrison AD. 2003. Chironomidae. In: Day J, Harrison AD, de Moor IJ, editors. *Guides to*  
639 *the Freshwater invertebrates of Southern Africa: Diptera*. Water Research Commission,  
640 Pretoria, South Africa. pp. 110-158.

641

642 Hassall C. 2014. The ecology and biodiversity of urban ponds. *Wiley Interdisciplinary*  
643 *Reviews: Water* 1: 187-206.

644

645 Hassall C, Anderson S. 2015. Stormwater ponds can contain comparable biodiversity to  
646 unmanaged wetlands in urban areas. *Hydrobiologia* 745: 137-149.

647

648 Heino J, Bini LM, Andersson J, Bergsten J, Bjelke U, Johansson F. 2017. Unravelling the  
649 correlates of species richness and ecological uniqueness in a metacommunity of urban pond  
650 insects. *Ecological Indicators* 73: 422-431.

651

652 Hill MJ, Heino J, Thornhill I, Ryves DB, Wood PJ 2017a. Effects of dispersal mode on the  
653 environmental and spatial correlates of nestedness and species turnover in pond communities.  
654 *Oikos* 126: 1575-1585.

655

656 Hill MJ, Biggs J, Thornhill I, Briers RA, Gledhill DG, White JC, Wood PJ, Hassall C. 2017b.  
657 Urban ponds as an aquatic biodiversity resource in modified landscapes. *Global Change*  
658 *Biology* 23: 986-999.

659

660 James KR, Cant B, Ryan T. 2003. Responses of freshwater biota to rising salinity levels and  
661 implications for saline water management: a review. *Australian Journal of Botany* 51: 703-  
662 713.

663

664 Knop E. 2016. Biotic homogenization of three insect groups due to urbanization. *Global*  
665 *Change Biology* 22: 228-236.

666

667 Legendre P. 2014. Interpreting the replacement and richness difference components of beta  
668 diversity. *Global Ecology and Biogeography* 23: 1324-1334.

669

670 Legendre P, Birks HJB. 2012. From classical to canonical conservation. Pages 201-248 in  
671 Birks HJB, et al., editors. Tracking environmental change using lake sediments. Springer,  
672 Dordrecht.

673

674 Li X, Chen G, Liu X, Liang X, Wang S, Chen Y, Pei F, Xu X. 2017. A new global land-use  
675 and land-cover change product at a 1-km resolution for 2010 to 2100 based on human–  
676 environment interactions. *Annals of the American Association of Geographers* 107: 1040-  
677 1059.

678

679 Lytle DA. 2015. Chapter 37: Order Hemiptera. Pages 1953-1979 in Thorp JH, Rogers DC,  
680 editors. Thorp and Covich's freshwater invertebrates: Ecology and general biology. Elsevier,  
681 Amsterdam.

682

683 Matthews GVT. 1993. The Ramsar Convention on Wetlands: its history and development.  
684 Ramsar Convention Bureau, Gland.

685

686 McKinney ML. 2008. Effects of urbanization on species richness: a review of plants and  
687 animals. *Urban ecosystems* 11: 161-176.

688

689 Mlambo MC, Bird MS, Reed CC, Day JA. 2011. Diversity patterns of temporary wetland  
690 macroinvertebrate assemblages in the south-western Cape, South Africa. *African Journal of*  
691 *Aquatic Science* 36: 299-308.

692

693 Mnaya B, Mwangomo E, Wolanski E. 2006. The influence of wetlands, decaying organic  
694 matter, and stirring by wildlife on the dissolved oxygen concentration in eutrophicated water  
695 holes in the Seronera River, Serengeti National Park, Tanzania. *Wetlands Ecology and*  
696 *Management* 14: 421-425.

697

698 Moges A, Beyene A, Ambelu A, Mereta ST, Triest L, Kelbessa E. 2017. Plant species  
699 composition and diversity in wetlands under forest, agriculture and urban land uses. *Aquatic*  
700 *Botany*, 138: 9-15.

701

702 Oksanen J, et al. 2017. *vegan: Community Ecology Package*. R package version 2.4-2.  
703 Retrieved from <https://CRAN.R-project.org/package=vegan>.

704

705 Paradis E, Schliep K. 2018. *ape 5.0: an environment for modern phylogenetics and*  
706 *evolutionary analyses in R*. *Bioinformatics* 35: 526-528.

707

708 Quantum GIS Development Team. 2017. *Quantum GIS Geographic Information System*.  
709 *Open Source Geospatial Foundation Project*. Retrieved from <http://qgis.osgeo.org>.

710

711 R Development Core Team, 2016. *R: A Language and Environment for Statistical*  
712 *Computing*. R Foundation for Statistical Computing, Vienna, Austria. Retrieved from  
713 <http://www.R-project.org/>.

714

715 Reavell P. 2003. Hemiptera. In: de Moor I, Day J, de Moor F, editors. *Guides to the*  
716 *Freshwater invertebrates of Southern Africa: Insecta II Hemiptera, Megaloptera,*

717 *Neuroptera, Trichoptera and Lepidoptera*. Water Research Commission, Pretoria, South  
718 Africa. pp. 16-71.  
719  
720 Reid AJ, et al. 2019. Emerging threats and persistent conservation challenges for freshwater  
721 biodiversity. *Biological Reviews* 94: 849-873.  
722  
723 Samways MJ, Simaika JP. 2016. *Manual of Freshwater Assessment for South Africa:*  
724 *Dragonfly Biotic Index*. Suricata 2. Pretoria South Africa, South African National  
725 Biodiversity Institute.  
726  
727 Seaman MT, Kok DJ, Watson M. 1999. Cladocera. In: Day JA, Stewart BA, de Moor IJ,  
728 Louw AE. *Guides to the Freshwater invertebrates of southern Africa: Crustacea I*. Water  
729 Research Commission, Pretoria, South Africa. pp. 81-110.  
730  
731 Soucek DJ, Dickinson A. 2012. Acute toxicity of nitrate and nitrite to sensitive freshwater  
732 insects, mollusks, and a crustacean. *Archives of Environmental Contamination and*  
733 *Toxicology* 62: 233-242.  
734  
735 Stals R. 2003. Coleoptera. In: Stals R, de Moor IJ, editors. *Guides to the Freshwater*  
736 *invertebrates of southern Africa: Coleoptera*. Water Research Commission, Pretoria, South  
737 Africa.  
738  
739 Suhling F, Müller O, Martens A. 2014. Namibian dragonflies: larval key and distribution.  
740 *Libellula Supplement* 13: 5-106.  
741

742 Suhling F, Sahlén G, Gorb S, Kalkman VJ, Dijkstra KDB, and van Tol J. 2015. Chapter 37:  
743 Order Odonata. Pages 1837-1914 in Thorp JH, Rogers DC, editors. Thorp and Covich's  
744 freshwater invertebrates: Ecology and general biology. Elsevier, Amsterdam.  
745

746 Tessier C, Cattaneo A, Pinel-Alloul B, Galanti G, Morabito G. 2004. Biomass, composition  
747 and size structure of invertebrate communities associated to different types of aquatic  
748 vegetation during summer in Lago di Candia (Italy). *Journal of Limnology* 63: 190-198.  
749

750 Thomaz SM, Ribeiro de Cunha E. 2010. The role of macrophytes in habitat structuring in  
751 aquatic ecosystems: methods of measurement, causes and consequences on animal  
752 assemblages' composition and biodiversity. *Acta Limnologica Brasiliensia* 22: 218-236.  
753

754 Thornhill IA, Biggs J, Hill MJ, Briers R, Gledhill D, Wood PJ, Gee JH, Ledger M, Hassall C.  
755 2018. The functional response and resilience in small waterbodies along land-use and  
756 environmental gradients. *Global change biology* 24: 3079-3092.  
757

758 Vavrek MJ. 2011. fossil: palaeoecological and palaeogeographical analysis tools. R package  
759 version 0.4.0. Retrieved from <https://CRAN.R-project.org/package=fossil>.  
760

761 Viana DS, et al. 2016. Assembly mechanisms determining high species turnover in aquatic  
762 communities over regional and continental scales. *Ecography* 39: 281-288.  
763

764 Williams DD. 2006. *The biology of temporary waters*. Oxford: Oxford University Press.  
765



766 Woodward RT, Wui Y. 2001. The economic value of wetlands: A meta-analysis. Ecological  
767 Economics 37: 257-270.  
768

769 Yee DA, Kehl S. 2015. Chapter 39: Order Coleoptera. Pages 2056-2154 in Thorp JH, Rogers  
770 DC, editors. Thorp and Covich's freshwater invertebrates: Ecology and general biology.  
771 Elsevier, Amsterdam.  
772

773 Yuan S, Li H, Dang Y, Liu C. 2017. Effects of triphenyl phosphate on growth, reproduction  
774 and transcription of genes of *Daphnia magna*. Aquatic Toxicology 195: 58-66.  
775

776 Zacharias I, Zamparas M. 2010. Mediterranean temporary ponds: a disappearing ecosystem.  
777 Biodiversity and Conservation 19: 3827-3834.  
778

779 Zedler JB, Kercher S. 2005. Wetland resources: Status, trends, ecosystem services, and  
780 restorability. Annual Review of Environment and Resources 30: 39-74.

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

784

	<b>Abundance</b>	<b>Sobs</b>	<b>Chao2</b>	<b>ICE</b> <sup>785</sup>
<b>Overall</b>	29872	22	25.6	23.7 <sup>786</sup>
<b>Zeekoevlei</b>	3399	17	19.5	18.9 <sup>787</sup>
<b>Rondevlei</b>	26473	16	18.0	17.5 <sup>788</sup>
				<sup>789</sup>

790

791 **Table 2** Model averaged estimates of local variables driving variation in overall species  
 792 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>					
<b>Conductivity</b>	<b>-0.0020</b>	<b>0.0006</b>	<b>-0.0033, -0.0008</b>	<b>0.5900</b>	<b>1</b>
<b>Nitrite</b>	<b>-193.9110</b>	<b>65.6108</b>	<b>-322.5059, -65.3161</b>	<b>0.5900</b>	<b>1</b>
<b>pH</b>	<b>-6.8909</b>	<b>2.9356</b>	<b>-12.6446, -1.1371</b>	<b>0.5900</b>	<b>1</b>
<b>Temperature</b>	<b>-1.8841</b>	<b>0.5639</b>	<b>-2.9894, -0.7788</b>	<b>0.5900</b>	<b>1</b>

793  
 794 Relative importance indicates the sum of Akaike weights over all models in the best model subset (models with  $\Delta AIC_C \leq 2$ , under each modelling scenario), in  
 795 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.  
 796 Significant traits (95% CI of the estimates does not cross the 0 threshold) are highlighted in bold text.

797

798 **Figure captions**

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

801

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

805

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

810 **Supplementary files**

811 **Online Resource 1** Shapiro-Wilks normality test and Mantel spatial autocorrelation test  
812 results for overall species richness, and species richness for Zeekoevlei and Rondevlei  
813 separately.

814

815 **Online Resource 2** Cross-correlation plots and Spearman's rank order correlation test results  
816 among % emergent vegetation cover, % submerged vegetation cover, conductivity ( $\mu\text{S cm}^{-1}$ ),  
817 pH, temperature ( $^{\circ}\text{C}$ ), dissolved oxygen concentration (mg/L), chlorine concentration  
818 (mg/L), phosphate concentration (mg/L), nitrite-nitrogen concentration (mg/L), *Escherichia*  
819 *coli* levels (cfu/100 ml) and faecal coliform levels (cfu/100 ml). Significance levels: \* :  $p <$   
820 0.05; \*\* :  $p < 0.01$ ; \*\*\* :  $p < 0.001$ .

821

822 **Online Resource 3** Species list of all macroinvertebrates sampled. 1: present; 0: absent.