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Additional Information

1 **MICROHABITAT PREFERENCES OF FISH**  
2 **ASSEMBLAGES IN THE UDZUNGWA**  
3 **MOUNTAINS (EASTERN AFRICA)**

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6

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20 **Running title: Microhabitat preferences of riverine fish assemblages in Africa**

21

22 **Abstract**

23 Environmental Flow Assessment (EFA) involving microhabitat preference models is a  
24 common approach to set ecologically-friendly flow regimes in territories with ongoing or  
25 planned projects to develop river basins, such as many rivers of Eastern Africa. However,  
26 habitat requirements of many African fish species are poorly studied, which may impair EFAs.  
27 This study investigated habitat preferences of fish assemblages, based on species presence-  
28 absence data from 300 microhabitats collected in two tributaries of the Kilombero River  
29 (Tanzania), aiming to disentangle differences in habitat preferences of African species at two  
30 levels: assemblage (i.e. between tributaries) and species (i.e. species-specific habitat  
31 preferences). Overall, flow velocity, which implies coarser substrates and shallower  
32 microhabitats, emerged as the most important driver responsible of the changes in stream-  
33 dwelling assemblages at the microhabitat scale. At the assemblage level, we identified two  
34 important groups of species according to habitat preferences: (i) cover-orientated and  
35 limnophilic species, including *Barbus* spp., Mormyridae and *Chiloglanis deckenii*, and (ii)  
36 rheophilic species, including *Labeo cylindricus*, *Amphilius uranoscopus* and *Parakneria*  
37 *spekii*. Rheophilic species preferred boulders, fast flow velocity and deeper microhabitats. At  
38 the species level, we identified species-specific habitat preferences. For instance, *Barbus* spp.  
39 preferred low flow velocity shallow depth and fine-to-medium substratum, whereas *L.*  
40 *cylindricus* and *P. spekii* mainly selected shallow microhabitats with coarse substrata.  
41 Knowledge of habitat preferences of these assemblages and species should enhance the  
42 implementation of ongoing and future EFA studies of the region.

43

44 Keywords: constrained additive ordination, environmental drivers, environmental flow  
45 assessment, fish communities, fuzzy rule-based system, stream-dwelling fish

46

## 47 1 Introduction

48 Worldwide river regulation by damming and water diversion has altered natural flow regimes (Poff et  
49 al., 1997), which negatively affects all living components of these ecosystems such as riparian  
50 vegetation, macrobenthos and fishes (Poff & Zimmerman, 2010). In the case of East Africa, rivers are  
51 less regulated compared to other parts of the world (McClain, Kashaigili, & Ndomba, 2013), but  
52 several factors, such as population growth, political stability and China's expanding interests, are  
53 triggering a significant increase in the construction of regulatory facilities and extraction of water to  
54 increase agriculture production (Cotula, 2012). Mitigating the impact of hydro development requires  
55 policy makers and managers to apply Environmental Flow Assessment (EFA) techniques to determine  
56 the quantities, quality, and patterns of water flows required to sustain freshwater ecosystem processes  
57 (i.e. the balance between ecosystem conservation and out-of-stream uses) (Arthington, Bunn, Poff, &  
58 Naiman, 2006). In this regard, holistic approaches for EFA that account for human needs and relate  
59 flow regime with abiotic (habitat) and biotic (fauna) changes are recommended (Petts, 2009; Poff et  
60 al., 2010). These relationships can be inferred in different manners, from simplified approaches  
61 covering fish assemblages (e.g. McClain et al., 2014) to complex data-demanding species-specific  
62 approaches (e.g. Alexander, Poulsen, Robinson, Ma, & Luster, 2018). In addition, EFA can be  
63 undertaken at different spatial scales (macro-, meso- or microhabitat scale) following different  
64 approaches (Poff et al., 2010), with approaches of small-to-intermediate scale and complexity being  
65 commonly used to carry out habitat-based EFA studies (Muñoz-Mas, Martínez-Capel, Schneider, &  
66 Mouton, 2012; Vezza, Parasiewicz, Rosso, & Comoglio, 2012). Here, we empirically investigated the  
67 fish preferences along gradients of habitat conditions at the microhabitat scale.

68 Fish habitat requirements have been widely studied (Akbaripasand & Closs, 2017; Allouche, 2002;  
69 Logez, Bady, & Pont, 2011); but African fish, including many endemic and endangered species, are  
70 often poorly studied and therefore information on the species may be often highly ambiguous and  
71 limited, but some notable exceptions exist (e.g. Gaigher, 1973; Ibanez et al., 2007; Kadye & Moyo,  
72 2008; Skelton, 2001). For instance, Kadye and Moyo (2008) demonstrated that the occurrence of  
73 riverine fish species is influenced by mesohabitat factors such as flow, depth and the type of  
74 substratum. This is in agreement with Kouamé et al. (2008), who found that canopy closure,  
75 leaves/wood, aquatic plants, temperature, width, total dissolved solids and depth should be considered  
76 as the main environmental drivers responsible of the variation in African fish assemblages. Other

77 studies performed at the microhabitat scale have assumed the relevance of at least the triad velocity-  
78 depth-substrata (Fukuda, De Baets, Waegeman, Verwaeren, & Mouton, 2013; Muñoz-Mas et al.,  
79 2012), but the importance of these individual physical factors may vary indicating different potential  
80 to discriminate fish presence (Gibson, 1993). Thus, species-specific habitat requirements in  
81 combination with environmental gradients shape the structure of stream fish assemblages from local  
82 to regional scales (Pease, Taylor, Winemiller, & King, 2015).

83 In the present study, we explore the microhabitat preferences and suitability for the riverine fish  
84 assemblage in two tributaries of the Kilombero River located in the foothills of the Udzungwa  
85 Mountains of Tanzania. The aims of this study were to (i) investigate the habitat preferences of the  
86 entire fish assemblage and (ii) provide a better knowledge about species-specific habitat preferences  
87 of riverine fishes of Africa with special emphasis in EFA studies. The patterns of association between  
88 fish species and environmental gradients presented in this study will improve our understanding about  
89 species assemblage structure of the region, which, in turn, is essential for future conservation and  
90 management actions of fish stocks and aquatic ecosystems.

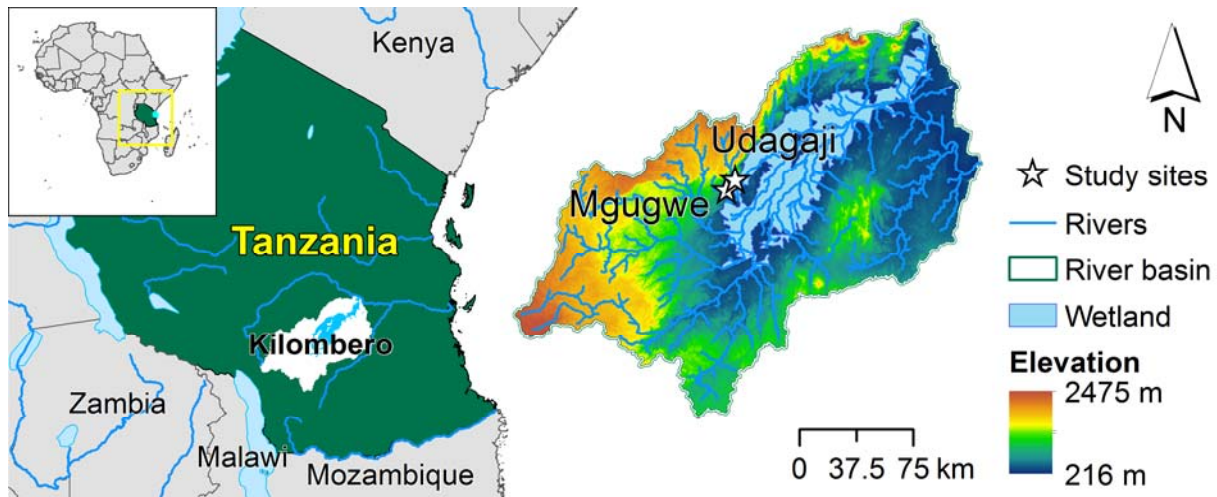
## 91 **2 Methods**

### 92 **2.1 Study area**

93 The Kilombero River Basin is characterised by a sub-humid tropical climate with relative humidity  
94 ranging from 70 to 80% with an annual rainfall of about 1200 to 1400 mm and two rainy seasons: a  
95 long rainy season in March to May and a shorter one around October to December (Mombo et al.,  
96 2011). Temperatures normally vary from 20 to 30 °C (Mombo et al., 2011). Human-related activities  
97 such as overgrazing by livestock, agriculture and human settlement are threatening the Kilombero  
98 River basin (Elisa, Gara, & Wolanski, 2010).

99 The sampled rivers were the Udagaji and Mgugwe, which are two small unregulated rivers that flow  
100 southwards from the Udzungwa Mountains National Park (FIGURE 1). The Udagaji catchment is  
101 densely forested whereas the Mgugwe catchment is naturally covered by forest and shrubs in similar  
102 proportions. Although the Udagaji River has been identified as a possible water source for a large  
103 irrigation scheme in the Kilombero Valley (see O’Keeffe et al., 2017), the basin area of the Mgugwe  
104 River is larger (213 vs. 25 km<sup>2</sup>). In accordance, the mean annual flow of the Mgugwe River

105 corresponds to 2.83 m<sup>3</sup>/s (1957-1991) whereas that of the Udagaji River corresponds to 0.81 m<sup>3</sup>/s  
106 (1957-1991). The minimum and maximum elevation of both sampled rivers did not differ significantly  
107 (300/325 and 1637/1802 m a.s.l., respectively) but the mean slope of the Udagaji River is more  
108 pronounced (20.2° vs. 16.3° in Mgugwe River), causing a flashier flow regime.



109

110 FIGURE 1. Location of the Udagaji and Mgugwe rivers within the African continent (left panels).  
111 Location of the Udagaji and Mgugwe rivers within the Kilombero River basin (right panel).

112 The lotic fish communities in this study area are composed of endemic catfish [*Amphilius uranoscopus*  
113 (Pfeffer, 1889), *Chiloglanis deckenii* (Peters, 1868) and *Schilbe moebiusii* (Pfeffer, 1896)], cyprinid  
114 [*Barbus* spp. and endemic *Labeo cylindricus* (Peters, 1852)], freshwater elephantfish [Mormyridae  
115 encompassing the genera *Hippopotamyrus*, *Marcusenius* and *Petrocephalus*] and endemic shellears  
116 [*Parakneria spekii* (Günther, 1868)]. Thus, fish communities in this territory are characterised by a  
117 high degree of endemism (additional information about the collected species is shown in Appendices  
118 S1 and S2).

119

## 120 2.2 Data collection

121 Sampling was carried out during the dry season to evaluate lower flows, when competitive interactions  
122 among fish species should be strongest (e.g. Sánchez-Hernández, Gabler, & Amundsen, 2017). In

123 accordance, the survey was undertaken during one week in the end of January 2015 (i.e. short dry  
124 season preceding the long rainy season).

125 Data collection (microhabitat and fish sampling) was replicated spatially (N = 300) across the Udagaji  
126 (N = 207) and Mgugwe (N = 93) rivers, starting in the midland part and ending in the mountainous  
127 part of the basins (see Appendix S1 for information about the number of occupied microhabitats and  
128 abundance for each fish species). The fish data were collected following the point abundance sampling  
129 approach (see Bain, Finn, & Booke, 1985 for details). This sampling approach is performed at the  
130 microhabitat scale and consists of electrofishing small plots ( $\approx 5 \text{ m}^2$ ), with homogeneous depth,  
131 velocity, substratum and cover, instead of larger and relatively heterogeneous mesohabitats such as  
132 pools or riffles. All fishes were identified *in situ* to the lowest taxon possible (mainly species level).

133 The standard approaches for Environmental Flow Assessment (EFA) at the microhabitat scale evaluate  
134 the habitat quality in scales between zero and one (Bovee et al., 1998), which typically requires further  
135 data transformation to deal with species abundances (e.g., Theodoropoulos, Skoulikidis, Stamou, &  
136 Dimitriou, 2018). Fish occupancy was low ( $2.30 \pm 0.37$  individuals per occupied microhabitat) (see  
137 Appendix S1) and a high number of microhabitats without fish catches were observed (N = 118), which  
138 prevented the use of abundance data. In addition, presence-absence models are usually more accurate  
139 than abundance models and often render convergent habitat preferences (Fukuda, Mouton, & De Baets,  
140 2011; Muñoz-Mas, Martínez-Capel, Alcaraz-Hernández, & Mouton, 2015, 2016). Therefore, fish  
141 captures were converted into presence-absence data (i.e. one if at least one specimen was observed in  
142 the sampled microhabitat or zero if none) for each of the 300 microhabitats surveyed and the  
143 exploratory analyses on microhabitat preferences was performed considering exclusively their  
144 presence or absence.

145 Regarding microhabitat measurements, depth (m) was measured with a wading rod (to the nearest cm)  
146 and the mean flow velocity of the water column – hereafter velocity (m/s) – was measured with a  
147 propeller current meter (OTT®) at the 40% of the measured depth. The percentage of each class of  
148 substratum was visually estimated around the sampling point following a simplification of the  
149 American Geophysical Union size scale, namely silt ( $<62 \mu\text{m}$ ), sand ( $62 \mu\text{m} - 2 \text{ mm}$ ), fine gravel (2–  
150 8 mm), gravel (8–64 mm), cobble (64–256 mm), boulder ( $> 256 \text{ mm}$ ) and bedrock (Muñoz-Mas et al.,  
151 2012). The substratum composition was converted into a single value through the dimensionless

152 substratum index (see Mouton, Alcaraz-Hernández, De Baets, Goethals, & Martínez-Capel, 2011).  
153 The abundance of 5 different types of cover: aquatic vegetation, reeds, log jams, shade and rocks,  
154 which summarize the concept of structural (e.g. large boulders, log jams) and escape cover (e.g. aquatic  
155 vegetation, reeds), was recorded and scored as absent, scarce, normal or abundant (i.e. from 0 to 3)  
156 (Muñoz-Mas, Papadaki, et al., 2016). In addition, the cover types and their scores were converted into  
157 the dimensionless cover index for the entire community by summing the different scores at each  
158 location (e.g. aquatic vegetation 0 + reeds 0 + log jams 0 + shade 0 + rocks 0 = 0, aquatic vegetation  
159 3 + reeds 0 + log jams 0 + shade 0 + rocks 1 = 4, etc.) (Muñoz-Mas, Papadaki, et al., 2016).

160 Finally, species-specific versions of the dimensionless cover index were calculated employing  
161 uniquely those cover types relevant for each target species, genus or family, which were determined  
162 after a  $\chi^2$  test between the presence-absence of the species and the analysed cover (Scheidegger &  
163 Bain, 1995), resulting in seven different cover-related variables one per species, genus or family. In  
164 microhabitat studies, cover is often used to characterise the habitat suitability (e.g. Johnson &  
165 Douglass, 2009; Muñoz-Mas et al., 2016). Therefore, a relatively large *p value* was selected (*p value*  
166 < 0.10) to avoid rejecting those cover types that presented weak associations with fish presence, which  
167 fits well the precepts applied for the analysis at the assemblage level where no selection was performed.  
168 The resulting species-specific versions of the cover index were used to reveal the most relevant  
169 microhabitat variables and their effect into the presence or absence of each target group in the species-  
170 specific analysis.

171

## 172 **2.3 Exploratory analyses on microhabitat preferences**

### 173 **2.3.1 Assemblage preferences – Constrained Additive Ordination (CAO)**

174 The general structure and microhabitat preferences of the fish assemblage was explored with  
175 Constrained Additive Ordination (CAO) (Yee, 2006). Unlike, Correlation or Canonical  
176 Correspondence analyses (CA & CCA), CAO does not involve any specific assumption – such as  
177 linearity or symmetry – on response curves (Yee, 2006), which may fit the ruling ecological gradient  
178 theory that disesteem either assumptions (Austin, 2007). In this regard, CAO has been considered more



179 reliable and demonstrated to be a proficient alternative to scrutinize the microhabitat requirements of  
180 sympatric competitor species (Vilizzi, Stakenas, & Copp, 2012).

181 CAO relates a *sample* × *species* matrix *Y* with a *sample* × *environmental variables* matrix *X*,  
182 and the output is an ordination plot (Vilizzi et al., 2012). In CAO, the resulting ordination plot depicts  
183 the distribution of a certain fish species, genus or family across the environmental gradient, so that the  
184 trend of the curve along this gradient or the presence of an optimum indicates the use/preference for  
185 certain values of the microhabitat variables (Vilizzi et al., 2012). In our ordination plot, the y-axis  
186 depicts the regression of the presence-absence data for each group of species on the environmental  
187 gradient (i.e. the summary of the collected microhabitat variables), which is plotted in the x-axis  
188 (Vilizzi et al., 2012). CAO was performed in *R* program (R Core Team, 2017) using the function *cao*  
189 in the package *VGAM* and the binomial link function (especially indicated for presence-absence) (Yee,  
190 2010). Pooled data (N = 300) were used to explore the assemblage preferences, although a CAO for  
191 each riverine system was also performed to investigate whether the microhabitat preferences of the  
192 fish assemblages varied between both rivers.

193

### 194 **2.3.2 Species specific habitat suitability – fuzzy rule-based systems (FRBSs)**

195 At the species level, models based on fuzzy logic (Zadeh, 1965), particularly Fuzzy Rule-Based  
196 Systems (FRBSs), have become the multivariate standard to develop habitat suitability models for  
197 EFA (e.g. Mouton et al., 2008; Muñoz-Mas, Papadaki, et al., 2016; Theodoropoulos et al., 2018).  
198 FRBSs are accurate and interpretable models because their accuracy is not at the expense of complex  
199 mathematical structures (Muñoz-Mas, Marcos-Garcia, et al., 2018). Their simplicity allows experts to  
200 modify the resulting FRBSs to cover a wider range of environmental conditions and/or variables  
201 (Mouton et al., 2008; Muñoz-Mas, Marcos-Garcia, et al., 2018). This emphasizes the usefulness of  
202 fuzzy logic to deal with the vague, imprecise and scarce data, typical of impoverished or extirpated  
203 freshwater fish populations (Muñoz-Mas et al., 2016). Here, presence-absence 0-order Takagi-Sugeno-  
204 Kang (TSK) fuzzy models were developed to explore the species-specific habitat preferences (Takagi  
205 & Sugeno, 1985) using the *R* program (see Muñoz-Mas, Marcos-Garcia, et al., 2018).

206 TSK fuzzy models consist of a series of fuzzy rules (more precisely IF-THEN sequences; see Novák  
207 & Lehmke, 2006) relating different categories (fuzzy sets) of the microhabitat variables, named to  
208 describe the environmental condition that they encompass (e.g. ‘low’, ‘medium’ or ‘high’ velocity),  
209 and the microhabitat suitability or fish presence-absence (Muñoz-Mas, Papadaki, et al., 2016). For  
210 instance, IF velocity is ‘low’ and depth is ‘medium’ and substrate is ‘medium’ THEN the microhabitat  
211 suitability = 1 (See TABLE 3 in *Results* section for examples on complete rule sets). Owing to the  
212 fuzzy nature of these sets the transition between them is mathematised with different membership  
213 functions to be gradual (i.e. a percentage between 0 and 1), which allows them to render smooth  
214 transitions between the evaluation performed on fully suitable/present (i.e. suitability = 1) and  
215 unsuitable/absence (i.e. suitability = 0) microhabitats. These gradual outputs are necessary to calculate  
216 the most usual indices of habitat quality (e.g. Weighted Usable Area – WUA) (Muñoz-Mas, Papadaki,  
217 et al., 2016). Finally, by providing the membership functions (type and parameters) and the list of  
218 fuzzy rules – considering all the possible combination of the fuzzy sets used to characterise each  
219 variable (i.e. rule *completeness*) (see Zhou & Gan, 2008) – these models can be fully replicated by  
220 EFA practitioners to evaluate hydraulic simulations in EFA studies (Mouton et al., 2008).

221 Developing TSK fuzzy models consists of determining i) the microhabitat variables included in the  
222 model (i.e. velocity, depth, substratum index and/or cover index), ii) the number of categories (e.g.  
223 two or three), iii) the parameters of the corresponding membership functions, which determine the  
224 amplitude and overlapping between categories, and iv) each rule consequent, which determines the  
225 suitability for every combination of variables and categories tested (suitability = 1 or suitability = 0)  
226 (Muñoz-Mas, Marcos-Garcia, et al., 2018).

227 Methodological recommendations for species distribution models indicate that at least 30 presence  
228 data are necessary to get reliable results (Wisniewski et al., 2008). In accordance, pooled data (presence-  
229 absence data of both rivers combined) for each fish species was used to infer the species-specific TSK  
230 fuzzy models. Accordingly, *C. deckenii* (N = 14), Mormyridae (N = 6) and *S. moebiusii* (N = 2) were  
231 dismissed. Additionally, selected species for modelling (*A. uranoscopus*, *Barbus* spp., *L. cylindricus*  
232 and *P. spekii*) appeared in a similar proportion of microhabitats in both rivers (see FIGURE 2 in *Results*  
233 section), which did not compromise the development of habitat suitability models.

234 Using the methods previously described (Muñoz-Mas, Marcos-Garcia, et al., 2018),  $\Pi$ -membership  
235 functions were selected to mathematise the categories of the input variables (also see Appendix S3).  
236 The four parameters of each of these functions were optimised with Differential Evolution (Ardia,  
237 Boudt, Carl, Mullen, & Peterson, 2011; Mullen, Ardia, Gil, Windover, & Cline, 2011; Storn & Price,  
238 1997) whereas the optimisation of the resulting rule consequents was nested within the optimisation  
239 of the membership functions and it was performed with the hill climbing algorithm (Mouton et al.,  
240 2008; Zhou & Gan, 2008). Thus, TSK fuzzy models were optimised for all the possible combinations  
241 from one variable to the complete set of four while model complexity was limited by considering two  
242 or three categories per input variable (i.e. ‘low’ and ‘high’ or ‘low’, ‘medium’ and ‘high’ for each  
243 microhabitat variable involved). As a consequence, a total of 80 models were developed for each taxon  
244 (species, genus or family). Then the most parsimonious TSK fuzzy model (i.e. the one balancing  
245 accuracy and complexity) was selected according to the information criteria ( $c = 2$ ) described by Yen  
246 and Wang (1998), which is based on the Akaike Information Criterion (AIC). Finally, an additional  
247 membership function corresponding to ‘very low’ depth was introduced to render null suitability to  
248 zero depth. In accordance, the consequent of each fuzzy rule involving this fuzzy set was set to zero  
249 (i.e. absence).

250 It should be kept in mind that species with more distinct environmental requirements are modelled  
251 better compared to species with wide tolerance (Somodi, Lepesi, & Botta-Dukát, 2017). Therefore, in  
252 addition to the weighted Mean Squared Error employed to optimise the TSK models several additional  
253 performance criteria were calculated (see Mouton, De Baets, & Goethals, 2010). Whence membership  
254 functions are optimised the linguistic labels no longer describe similar microhabitat characteristics and  
255 they do not allow direct comparison (Zhou & Gan, 2008). In accordance, univariate partial dependency  
256 plots (Friedman, 2001) were developed to get a general depiction of the modelled species-specific  
257 microhabitat suitability.

258

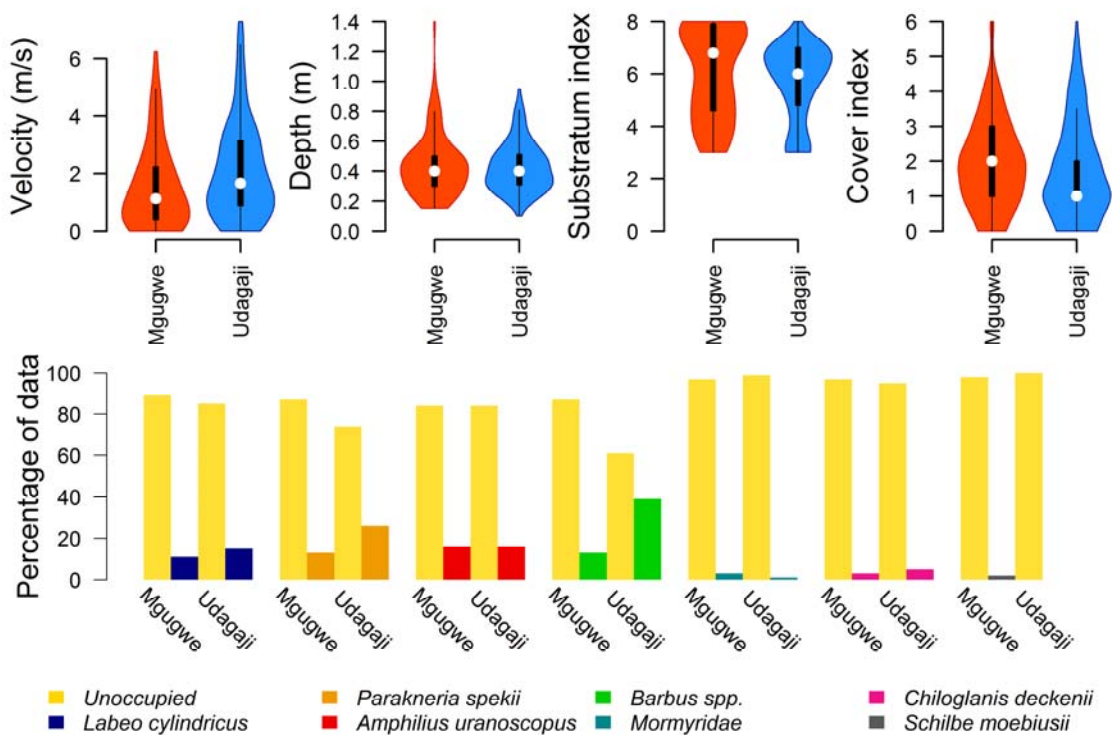
### 259 **3 Results**

260 Overall, both river systems presented similar distributions of the microhabitat variables, but with some  
261 minor differences as microhabitats sampled in the Udagaji River presented velocities slightly higher

262 than the Mgugwe River (FIGURE 2 upper panel). In contrast, the Mgugwe River had a coarser  
 263 substratum and the cover more abundant.

264 Species appeared in similar proportion of microhabitats in both riverine systems and thus, fish  
 265 community was similar across rivers, with the exception of the endemic *S. moebiusii*, which was only  
 266 incidentally captured in the Mgugwe River (see lower panel of FIGURE 2). However, the species-  
 267 specific cover index acknowledged some differences in the relevant cover among fish species  
 268 (Appendix S1).

269



270

271 F I G U R E 2. Violin plots of the microhabitat variables collected in Udagaji and Mgugwe rivers  
 272 (upper panel). Percentage of occupied and unoccupied microhabitats stratified per species and river  
 273 (lower panel).

274

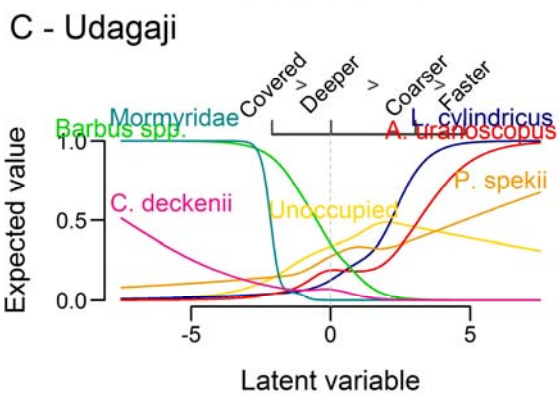
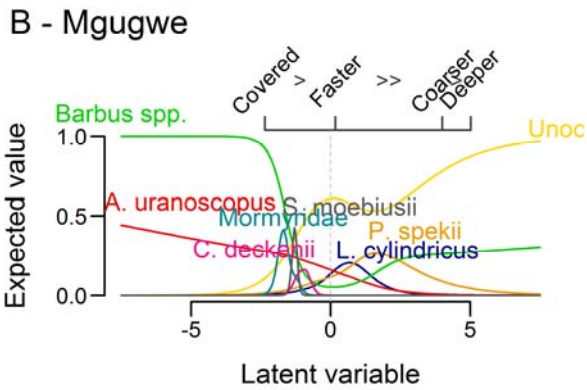
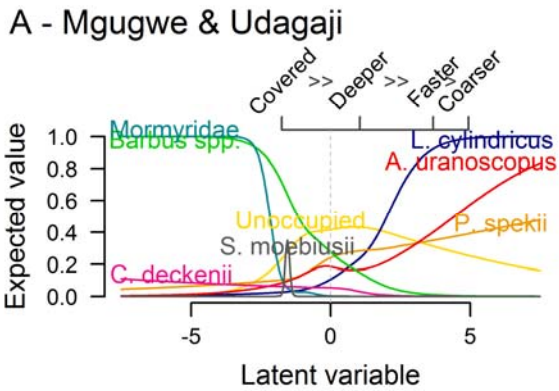
### 275 3.1 Assemblage preferences – Constrained Additive Ordination (CAO)

276 According to pooled data, substratum index had the greatest influence (right extreme of the  
277 environmental gradient) on fish assemblage (TABLE 1 and FIGURE 3). Depth (Mgugwe River) and  
278 velocity (Udagaji River) emerged as the strongest predictors of fish assemblage, but with substratum  
279 index showing a remarkable influence on the environmental gradients (FIGURE 3). The other extreme  
280 of the gradient (left) was common in all cases and dominated by the cover index (TABLE 1).

281 Overall, the ordination identified two broad groups of species based on its location with respect to the  
282 latent variable: (i) cover-orientated and limnophilic group (left part) which includes *Barbus* spp.,  
283 Mormyridae and *C. deckenii* and (ii) rheophilic group (right part) which includes *L. cylindricus*, *A.*  
284 *uranoscopus* and *P. speki* (FIGURE 3A). For example, *Barbus* spp. occurrence was mainly  
285 characterized by high cover index, and fine substrata, low flow velocity and shallow depth (FIGURE  
286 3A). In contrast, the occurrence of *L. cylindricus* was determined by the presence of coarse substrata  
287 (i.e. boulders and bedrock), fast flow velocity and larger depth, and, accordingly, low cover index.  
288 *Schilbe moebiusii* was set in an intermediate location, showing a clear dependence of unoccupied  
289 microhabitats.

290 The river specific CAOs rendered similar distribution patterns (FIGURE 3B & 3C). Therefore, in the  
291 Mgugwe River, *Barbus* spp., followed by Mormyridae, *S. moebiusii* and *C. deckenii*, were ordinated  
292 along the environmental gradient dominated by cover index whereas *L. cylindricus* and *P. speki*  
293 tended to avoid deeper and coarsest (i.e. bedrock) microhabitats. In the Udagaji River this aggregation  
294 appeared even more marked. The only discrepancy occurred for *A. uranoscopus*, which was ordinated  
295 in different groups in each river.

296 [TABLE 1] (find tables after References section)



297

298 FIGURE 3. Constrained additive ordination plot for the fish assemblage present in the Udagaji and  
 299 Mgugwe rivers: (a) pooled, (b) Mgugwe River and (c) Udagaji River.

300

301 **3.2 Species specific habitat suitability models – fuzzy rule-based systems**

302 TSK models presented a general accuracy (CCI) above 60% and were over-predictive (sensitivity >  
 303 specificity), with sensitivity being higher than 70% in all cases (TABLE 2). On the basis of the  
 304 performance criteria, *L. cylindricus* presented the most species-specific habitat preferences and *A.*

305 *uranoscopus* the least, which is in agreement with the discrepant ordinations obtained in the analyses  
 306 performed on each river separately (FIGURE 3B & 3C).

307 The best predictor variables, number of fuzzy sets (categories) and the shape of the corresponding  
 308 membership functions varied among species (FIGURE 4 & TABLE 3), which indicates different  
 309 environmental drivers of species presence and range of tolerance. Nevertheless, the fuzzy sets for depth  
 310 (*Barbus* spp. versus *L. cylindricus*) and for substratum (*Barbus* spp. versus *P. spekii*) partially  
 311 coincided, indicating similar environmental thresholds for these species. The most parsimonious  
 312 model for *Barbus* spp., which presented the largest sample size (N = 93), involved the largest number  
 313 of fuzzy rules (i.e. 12) whereas those for *L. cylindricus* (N = 42) and *A. uranoscopus* (N = 48) involved  
 314 respectively only six and three rules. *Barbus* spp. preferred low flow velocity shallow depth and fine-  
 315 to-medium substratum, whereas *L. cylindricus* and *P. spekii* mainly selected shallow microhabitats  
 316 with coarse substrata, although the latter shunned bedrock substrata (FIGURE 5). *Amphilius*  
 317 *uranoscopus* preferred shallow microhabitats.

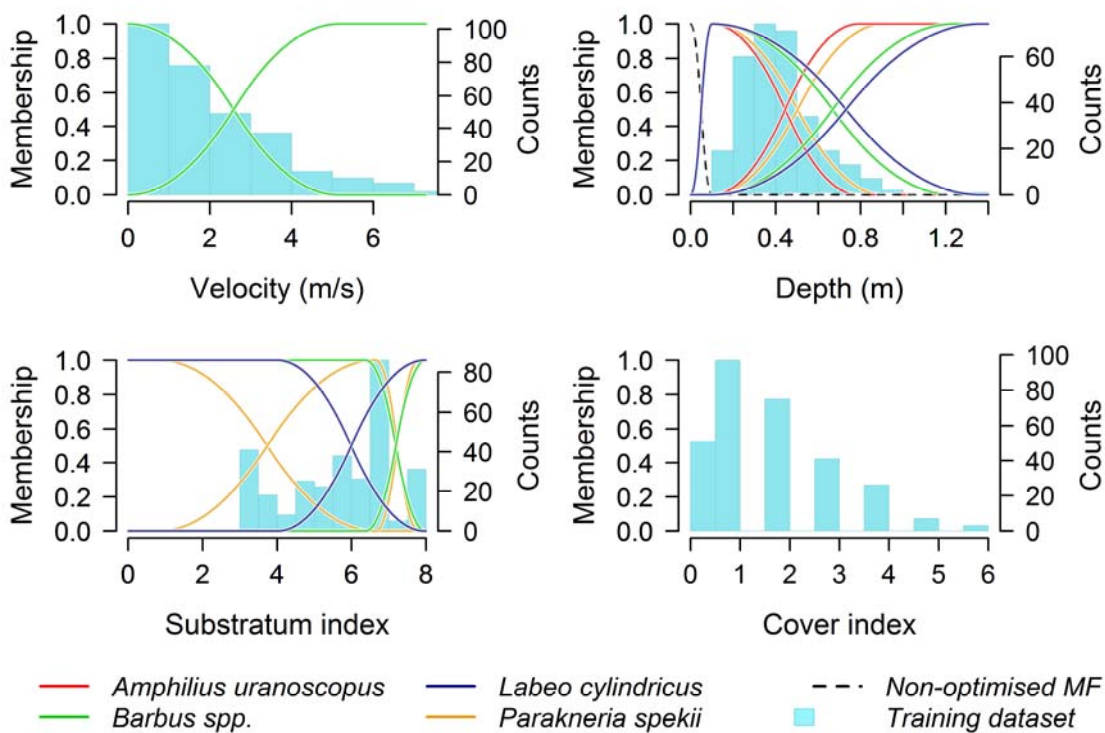
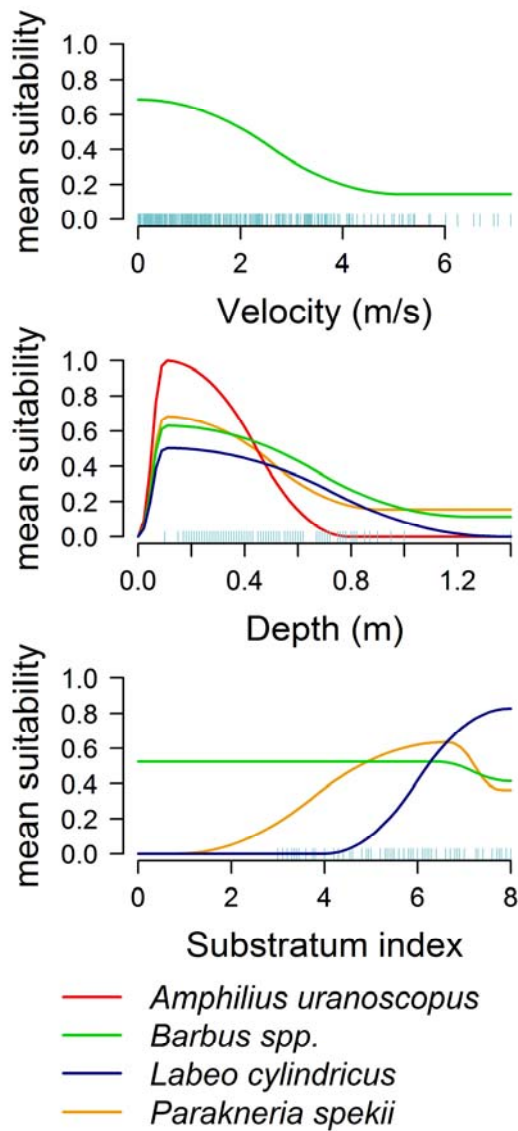


FIGURE 4. Optimal number of fuzzy sets (categories) and their corresponding membership functions for the most parsimonious 0-order Takagi–Sugeno–Kang fuzzy rule-based models obtained

321 with Differential Evolution (numeric values characterising each membership function can be consulted  
 322 in Supporting information Appendix S3). The membership function including zero depth (very low,  
 323 VL) was not optimised (dashed line). The distribution of each variable in the training data set (pooled  
 324 data) is depicted by the blue bars in the background.

325 [TABLE 3]



326

327 F I G U R E 5. Partial dependency plots for the most parsimonious 0-order Takagi–Sugeno–Kang  
 328 fuzzy rule-based models of those species with sufficient sample size ( $N > 30$ ). Ticks close to the x-  
 329 axis depict training data.



## 330 4 Discussion

331 A central challenge in community ecology is to understand the mechanisms that shape animal  
332 assemblages. Our study corroborated that, in the foothill rivers of the Udzungwa Mountains, the  
333 occurrence of different fish assemblages is mainly influenced by microhabitat factors such as the type  
334 of substratum, flow velocity and the availability of cover (Kadye & Moyo, 2008). In addition, we  
335 identified differences and similarities in specific habitat preferences among fish species, which is  
336 essential for the conservation and effective management of these fish stocks on the basis of future  
337 Environmental Flow Assessments (EFAs). From an applied perspective, the results obtained through  
338 Constrained Additive Ordination (CAO) may be especially useful in studies encompassing longer river  
339 segments where habitats are classified in broad categories such as riffles, banks or pools (e.g. McClain  
340 et al., 2014) that may resemble meso-scale studies (e.g. Vezza et al., 2012). Conversely, the TSK fuzzy  
341 models may be particularly indicated to detailed-scale studies where shorter river segments are of  
342 special interest as it is typically done in EFA studies involving physical habitat simulation approaches  
343 (Reiser & Hilgert, 2018). Thus, this study exemplified how different analysis techniques could be  
344 useful to resource managers for making specific decisions in line with the habitat preferences of fish  
345 species and assemblages. In such context, CAO methods emerged as the best technique for most  
346 resource managers, whereas TSK fuzzy models may require more specialised practitioners.

347

### 348 4.1 Assemblage preferences – Constrained Additive Ordination (CAO)

349 We revealed similarities in habitat preferences among fish species. Outcomes from CAO indicated the  
350 presence of two major groups of species. The first group encompassed species with cover-orientated  
351 and limnophilic preferences (i.e. *Barbus* spp., *C. deckenii* and Mormyridae), avoiding microhabitats  
352 with coarse substrata and high flow velocity. The second group encompassed the rheophilic species,  
353 which take advantage of boulders presence to endure high velocity (i.e. *L. cylindricus*, *P. spekii* and *A.*  
354 *uranoscopus*). This ordination between rheophilic and limnophilic stream-dwelling fish species based  
355 on preferred microhabitats (e.g. velocity and cover) is common worldwide (e.g. Allouche, 2002;  
356 Vadas, Vadas, & Orth, 2000) as well as in other African basins (Kadye & Moyo, 2008), which  
357 highlights the key role of velocity and cover in understanding the patterns of association between fish  
358 species and environmental gradients.

359 Regarding the limnophilic group, our findings are in agreement with previous studies covering species  
360 of the genus *Barbus* and the family Mormyridae, which indicated affinity of these taxa for slow flow  
361 habitats with fine substrata (Eccles, 1992; Kadye & Moyo, 2008). Furthermore, *Barbus* spp. and  
362 Mormyridae usually have a clear preference for vegetated inshore microhabitats (Bell-Cross &  
363 Minshull, 1988; Worthington, 1929), which is in agreement with the most relevant cover types  
364 indicated by the  $\chi^2$  test (see supplementary material appendix S1) that are prone to occur near banks  
365 (Schoelynck et al., 2018). In contrast, we observed that *C. deckenii* may not follow the same habitat  
366 preferences as other related species that usually show a clear habitat preference for rapids (Eccles,  
367 1992; Gaigher, 1973; Roberts, 1975; Schmidt, Bart, & Nyngi, 2015). However, ambiguous outcomes  
368 have been found for other species of the genus (e.g. *C. brevibarbis* Boulenger, 1902); showing a wide  
369 use of different habitats such as rapid waters (i.e. rocks and small boulders in flowing water), woody  
370 debris and exposed roots along the river bank and emergent stands of vegetation in the middle of a  
371 sandy channel (Schmidt et al., 2015). Thus, in accordance with our results and previous works on  
372 species of this genus, we posit that *C. deckenii* should be considered as a eurytopic species with ample  
373 microhabitat preferences.

374 The rheophilic group is in line with previous knowledge on related species (Gaigher, 1973; Kadye &  
375 Moyo, 2008). *Labeo cylindricus* led the ordination by showing the highest affinity to the presence of  
376 rocky substrata and the occurrence of fast flow velocity, which is in line with previous studies  
377 (Gaigher, 1973). *Parakneria spekii* showed, conversely, a weaker relationship with the environmental  
378 gradient, which indicates no marked preferences within mountain river segments that inherently  
379 involve coarser substrata and faster flow velocities. Little is known about the preferred microhabitats  
380 of *A. uranoscopus*, but researchers agree that rocky habitats of flowing waters are preferred (Ngugi,  
381 Manyala, Njiru, & Mlewa, 2009; Skelton, 2001) as in other species of this genus (Gaigher, 1973).  
382 However, the abundance of roots of riparian trees facilitates the presence of *A. uranoscopus* (van  
383 Oosterhout, van der Velde, & Gaigher, 2009). This could explain why the species was differently  
384 ordinated between the Mgugwe and Udagaji Rivers. In this regard, it should be noted that aquatic  
385 vegetation is only present in the Mgugwe River (Muñoz-Mas, Sánchez-Hernández, et al., 2018) where  
386 *A. uranoscopus* tended to select microhabitats with cover. A  $\chi^2$  test for aquatic vegetation was  
387 performed for each river separately and that considering only the data collected in the Mgugwe River  
388 remained not significant in *A. uranoscopus*. Nevertheless, we consider it is still possible that aquatic

389 vegetation could be a refuge selected by *A. uranoscopus* because 66% of the occupied microhabitats  
390 in that river ( $p$  value = 0.24) were under this cover type. In accordance, the species may show predation  
391 risk-driven changes in habitat use linked with the presence and absence of cover (e.g. aquatic  
392 vegetation) as it has been widely observed in other fish species (e.g. Camp, Gwinn, Pine III, & Frazer,  
393 2011). On the other hand, other factors not covered in this study – such as for example interspecific  
394 competition – may also be responsible for differences in habitat requirements of many fish species  
395 among riverine systems and should receive further attention. Finally, *S. moebiusii* was ordinated as a  
396 species with limnophilic preferences. Despite the low sample size (i.e. two), which prevented reliable  
397 conclusions about its preferences, there are some examples within this family showing preference for  
398 deep pools (Kadye & Chakona, 2012).

399

#### 400 **4.2 Species specific habitat suitability – fuzzy rule-based systems (FRBSs)**

401 Based on the acknowledged correlation between the specificity of the habitat preferences and models’  
402 performance (Somodi et al., 2017), the species-specific fuzzy rule-based systems indicated that *L.*  
403 *cylindricus* has the most specific habitat preferences whereas *A. uranoscopus* the least. This conclusion  
404 is supported by the absolute values of the performance criteria, which were similar or higher than those  
405 obtained in previous studies on this research topic (Fukuda et al., 2013; Muñoz-Mas et al., 2016).  
406 Microhabitat studies almost systematically assumed the relevance of at least the triad velocity-depth-  
407 substratum (Fukuda et al., 2013; Garbe, Beevers, & Pender, 2016; Reiser & Hilgert, 2018), although  
408 the relevance of cover has occasionally been assumed too (Allouche, 2002; Johnson & Douglass, 2009;  
409 Muñoz-Mas, Papadaki, et al., 2016). These variables are acknowledged as the most important at the  
410 microhabitat scale (Gibson, 1993), but a few of them could be occasionally redundant as it has herein  
411 been demonstrated. This highlights the advisability of testing different model structures (i.e. input  
412 variables’ set and number of fuzzy sets and membership functions) to obtain parsimonious models at  
413 the microhabitat scale (Muñoz-Mas et al., 2016) as in this study. Noteworthy, the most complex TSK  
414 fuzzy model was obtained for *Barbus* spp., which in turn presented the largest sample size, while for  
415 species of inferior sample sizes (e.g. *L. cylindricus* or *A. uranoscopus*) the most parsimonious TSK  
416 fuzzy models were markedly simpler; altogether suggesting an adequate trade-off between model  
417 parameterization and sample size of the Yen and Wang approach (1998).

418 Fuzzy rule-based models fitted well with those results obtained using CAO, although velocity and,  
419 especially, cover were underrepresented because three out of four models were addressed to the  
420 rheophilic group. Previous studies comparing CAO with species-specific models rendered disparate  
421 results, which suggests that further research is needed to advocate one or another approach (Baselga  
422 & Araújo, 2009; Maguire et al., 2016). Nevertheless, the ultimate TSK fuzzy models rendered a similar  
423 broad picture compared to CAO. For example, *Barbus* spp. selected low flow velocity, shallow depth  
424 and fine-to-medium substratum and the rheophilic group appeared in shallow microhabitats with  
425 coarse substrata. The extreme case was *A. uranoscopus* for whom the most parsimonious models  
426 employed exclusively depth. That said, the application of the approach (fuzzy rule-based models)  
427 described in the present study may usefully be extended to other territories, in which the identification  
428 of habitat preferences is of topical importance.

### 429 4.3 Conclusions

430 As a caveat, caution should be exercised regarding conclusions from this study because our analyses  
431 only included two riverine systems. Yet, the promising results of this study encourage the extension  
432 of this approach to other riverine systems to corroborate or refute our conclusions. We proved that  
433 analyses through Constrained Additive Ordination (CAO) enable a high-quality exploration of the  
434 habitat preferences of the fish assemblages present in the foothill streams of the Udzungwa Mountains.  
435 Conversely, scrutinising the microhabitat preferences exclusively at the species level with Takagi-  
436 Sugeno-Kang (TSK) fuzzy models may have rendered an impaired picture about the habitat  
437 preferences of the studied fish community because a minimum number of observations (i.e. at least  
438 30) are necessary to optimise them (Wisiz et al., 2008). The information obtained with CAO shall  
439 greatly assist Environmental Flow Assessment (EFA) studies where the impact of river regulation is  
440 carried out semi-quantitatively (e.g. McClain et al., 2014). However, the inability to describe  
441 quantitatively the relationship between flow regime and ecological response to infer the benefits of  
442 environmental flows has been pointed out as a limitation of current EFA approaches (Webb, de Little,  
443 Miller, & Stewardson, 2018). In the future, the conflicts associated with water resources and its  
444 allocation are expected to increase (Dudgeon, 2000; McClain et al., 2013), which may compel some  
445 stakeholders to express doubts about the accuracy of these semi-quantitative EFAs. Previous  
446 approaches based on the physical habitat simulation that evaluate representative river segments with  
447 microhabitat preference models – such as the fuzzy rule-based models present in this study – have

448 been stated to be the most defensible approach from a legal perspective (Reiser & Hilgert, 2018;  
449 Tharme, 2003), rendering the numeric outputs necessary to overcome inaccuracy and biases linked to  
450 personal opinions. In accordance, results based on fuzzy rule-based models should be more credible  
451 to support more ecologically-friendly alternatives in conflicting EFA such as, for instance, in regions  
452 where environmental flows lead to significant monetary losses (e.g. Cheng & Li, 2018). Nonetheless,  
453 it should be noted that the use of physical habitat simulation approaches has been included in national  
454 legislative frameworks (Muñoz-Mas, Papadaki, et al., 2016) and could promptly be included in the  
455 legislation of African countries including environmental rules regarding flows (e.g. South Africa,  
456 Kenya and Tanzania) (McClain et al., 2013). Therefore, the combined analysis of the habitat  
457 preferences at the assemblage and species level analysis should provide valuable information to  
458 adequately assist further studies on microhabitat preferences and EFAs.

459

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475

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707

708 **Authors' Contribution Statement**

709 Conceived and designed the investigation: RMM, FMC, RT, MEMc. Performed field and/or laboratory  
710 work: RMM, RT, SM, RM. Analysed the data: RMM. Contributed materials, reagents, and/or analysis  
711 tools: RMM. Wrote the paper: RMM, JSH, FMC, MEMc.

712

713 **Tables**

714 TABLE 1 Loads for each variable in Constrained Additive Ordination (CAO) according to the  
 715 environmental gradient.

Variable	Environmental gradient		
	Pool	Mgugwe	Udagaji
Cover index	-0.234	-0.314	-0.28
Depth	0.140	0.669	0.002
Velocity	0.489	0.023	0.639
Substratum index	0.658	0.533	0.406

716

717 TABLE 2 Performance for the most parsimonious 0-order Takagi-Sugeno-Kang fuzzy rule-  
 718 based models of those species with sufficient sample size ( $N > 30$ ): weighted Mean Squared  
 719 Error (wMSE), accuracy or Correctly Classified Instances (CCI), Sensitivity (Sn), Specificity  
 720 (Sp) and True Skill Statistics (TSS).

Species	wMSE	CCI	Sn	Sp	TSS
<i>Amphilius uranoscopus</i>	0.23	0.62	0.73	0.60	0.32
<i>Barbus</i> spp.	0.21	0.65	0.74	0.61	0.36
<i>Labeo cylindricus</i>	0.18	0.68	0.81	0.66	0.47
<i>Parakneria spekii</i>	0.22	0.62	0.74	0.59	0.33

721



722 TABLE 3 Fuzzy rules for the most parsimonious 0-order Takagi-Sugeno-Kang fuzzy rule-  
 723 based models of those species with sufficient sample size. The labels for the optimised fuzzy  
 724 sets correspond to ‘very low’ (VL), ‘low’ (L), ‘medium’ (M) and ‘high’ (H). The membership  
 725 function and the consequent for the fuzzy set corresponding to VL depth remained constant.  
 726 Notice that each species varies in the variables and number of fuzzy sets and hence in the  
 727 ultimate number of fuzzy rules. Rule consequents can be interpreted as absence (0) or presence  
 728 (1).

Species	Rule	Velocity	Depth	Substratum index	Cover index	Consequents
<i>Amphilius uranoscopus</i>	1	-	VL	-	-	0
	2	-	L	-	-	1
	3	-	H	-	-	0
<i>Barbus spp.</i>	1	L	VL	L	-	0
	2	H	VL	L	-	0
	3	L	L	L	-	1
	4	H	L	L	-	0
	5	L	H	L	-	0
	6	H	H	L	-	0
	7	L	VL	H	-	0
	8	H	VL	H	-	0
	9	L	L	H	-	0
	10	H	L	H	-	1
	11	L	H	H	-	1
	12	H	H	H	-	0
<i>Labeo cylindricus</i>	1	-	VL	L	-	0
	2	-	L	L	-	0
	3	-	H	L	-	0
	4	-	VL	H	-	0
	5	-	L	H	-	1
	6	-	H	H	-	0

	1	-	VL	L	-	0
	2	-	L	L	-	0
	3	-	H	L	-	0
	4	-	VL	M	-	0
<i>Parakneria spekii</i>	5	-	L	M	-	1
	6	-	H	M	-	0
	7	-	VL	H	-	0
	8	-	L	H	-	0
	9	-	H	H	-	1

729

## **Supplementary information**

List of items in the supplementary:

- Appendix S1. Summary of the assemblage composition present in the Udagaji and Mgugwe Rivers (Kilobero River Basin - Tanzania).
- Appendix S2. Summary of the habitat preferences and biology of the captured taxa (species, genus or family) based on previous literature. Given the paucity of available info, the summary also includes references of Eastern and Southern Africa.
- Appendix S3. Membership function parameters in fuzzy rule-based systems.

**Appendix S1. Summary of the assemblage composition present in the Udagaji and Mgugwe Rivers (Kilobero River basin – Tanzania). \*Only significant ( $p$  value <0.1) relevant covers based on species-specific cover index ( $\chi^2$  test) are shown.**

Scientific name	Common name (English/Kiswahili)	Endemic to Africa	Development stage of the captured specimens [size range]	Number of occupied microhabitats ( $N_{\text{presence}}$ )	Microhabitat fish occurrences (Mean number of individual)	Relevant cover ( $\chi^2$ test)*
<i>Amphilius uranoscopus</i> (Pfeffer, 1889)	Mountain catfish/Kolokolo	Yes	Adult [8.5-14.5 cm]	48	1.35±0.20	-
<i>Barbus</i> spp.	Barbels/Dagaa	-	Juvenile [1.5-6.9 cm]	93	3.42±0.96	Reeds Shade Aq. vegetation
<i>Chiloglanis deckenii</i> (Peters, 1868)	Pangani suckermouth	Yes	Adult [4.3-7.0 cm]	14	1.43±0.63	Shade
<i>Labeo cylindricus</i> (Peters, 1852)	Redeye labeo/Ningu	Yes	Juvenile [8.5-13.6 cm]	42	1.29±0.19	Rocks Shade
Mormyridae	Freshwater elephantfishes/Ndipi	Yes	Adult [9.2-14.6 cm]	6	1.00±0.00	Reeds Shade
<i>Parakneria spekii</i> (Günther, 1868)	-	Yes	Adult [3.6-5.2 cm]	66	2.39±0.55	Aq. vegetation
<i>Schilbe moebiusii</i> (Pfeffer, 1896)	Nembe	Yes	Juvenile [6.5-14.4 cm]	2	1.00±0.00	-

**Appendix S2. Summary of the habitat preferences and biology of the captured species, genus or family based on previous literature. Given the paucity of available info, the summary also includes references of Eastern and Southern Africa.**

Scientific name	Species, genus or family biology
<i>Amphilius uranoscopus</i> (Pfeffer, 1889)	Small (max. length < 17 cm) mountain-climbing/orobatic fish located in the headwater of riverine systems and usually restricted to high altitude sections with high flow conditions and coarse substratum (Ngugi, Manyala, Njiru, & Mlewa, 2009; Roberts, 1975). The species prefers clear, flowing water in rocky habitats feeding on macrozoobenthos (Skelton, 2001).
<i>Barbus</i> spp.	The African genus presents the largest amount of species (Tsigenopoulos, Ráb, Naran, & Berrebi, 2002), some of them suffering a marked process of miniaturization (Conway, Kubicek, & Britz, 2017). They prefer vegetated inshore and/or littoral waters, with either hard or soft substratum (Stewart & Murray, 2017). The small specimens of this genus have mostly been related to slow and shallow habitats with silty and sandy substratum (Kadye & Moyo, 2008).
<i>Chiloglanis deckenii</i> (Peters, 1868)	Small species (max. length < 7 cm) that usually prefers fast flowing conditions (Eccles, 1992). Because <i>Chiloglanis</i> spp. possess distinctive oral discs to feed and maintain their position in flowing waters (Schmidt, Bart, & Nyingi, 2015), they are considered to be mountain-climbing/orobatic fishes (Roberts, 1975). Some specimens of the genus have been collected near rocks in fast flowing conditions (Schmidt et al., 2015).
<i>Labeo cylindricus</i> (Peters, 1852)	This intermediate species (max. length < 40 cm) lives in both sediment-free and sediment-rich rocky riverine habitats with clear and running waters, but also inhabiting lakes and reservoirs (Bell-Cross & Minshall, 1988). The species feeds on periphyton (mainly diatoms) and other small algae from the rocks, tree trunks and other firm surfaces (Skelton, 2001). It is a potamodromous species that migrates upstream in shoaling groups to breed (Weyl, Finlayson, Impson, Woodford, & Steinkjer, 2014), using the mouth and broad pectorals to climb damp surfaces of barrier rocks and weirs (Skelton, 2001). <i>Labeo</i> sp. seemed more capable of migrating during higher flows than any other co-occurring species (Bowmaker, 2013).
Mormyridae	Many mormyrids appear to be potamodromous thus, they leave large lakes or rivers to migrate into smaller streams and flooded areas for spawning (Hopkins, 1986). Juvenile mormyrids are then captured in the rivers and pools next to these habitats at the beginning of the dry season (Hopkins, 1986). Some species, particularly the small riverine species, tend to move in large mixed-species schools (Hopkins, 1986). For example, <i>Marcusenius livingstonii</i> is an intermediate species (max. length < 30 cm) that occurs in quiet waters of rivers, moving on to flood plains to breed

(Eccles, 1992). *Petrocephalus* cf. *steindachneri* is a small species (probable max. length < 12 cm), which is likely to occur mainly in shallow and muddy waters, sheltered bays, lagoons, and swampy areas, preferring quiet parts of rivers where there is abundant vegetation (Bell-Cross & Minshull, 1988). In lacustrine habitats, some species, such as *Hippopotamyrus* cf. *grahami* (max. length < 25 cm), may prefer shallow and coastal waters with sand as substratum (Greenwood, 1966). This species frequents areas overgrown by water lilies (Worthington, 1929). Conversely other species of the genus are found in rocky habitats in flowing waters (Skelton, 2001).

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*Parakneria spekii*  
(Günther, 1868)

Small species (max. length < 6.2 cm) that inhabits upland streams and pools (Eccles, 1992; Seegers, 1995). As a omnivorous fish species, the species feeds on a wide variety of food resources such as algae, small insect larvae and crustaceans, but showing a clear preference for algae when it is available (Seegers, 1995). Other species of this genus show a notable preference for small pools with a rocky bottom of small flowing streams with cool and clear water (Kleynhans, 1988).

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*Schilbe moebiusii*  
(Pfeffer, 1896)

Small riverine fish species (max. length < 26 cm) with some examples within this family showing a clear preference for lentic areas (deep pools) (De Vos, 1995; Eccles, 1992; Kadye & Chakona, 2012).

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### Appendix S3. Membership function parameters in fuzzy rule-based systems.

The relationship of the input variables with the corresponding fuzzy set was mathematised by means of  $\Pi$ -membership functions (Equation 1 and Figure 1).  $\Pi$ -membership functions are defined by four parameters ( $a_m$ ,  $b_m$ ,  $c_m$  and  $d_m$ ), although when  $b_m$  equals  $c_m$  the membership functions present a single maxima at this point. In addition to the variable selection, these parameters were optimised with Differential Evolution (Storn & Price, 1997). The graphical depiction of the resulting membership functions can be consulted within the main text whereas the numeric results are depicted in Table 1.

Storn R., & Price K. (1997). Differential Evolution – A Simple and Efficient Heuristic for global Optimization over Continuous Spaces. *Journal of Global Optimization*, 11, 341–359. doi: 10.1023/A:1008202821328

$$\mu(x; a, b, c, d) =$$

$$= \left\{ \begin{array}{l} 0, x \leq a \\ 2 \left( \frac{x-a}{b-a} \right)^2, a \leq x \leq \frac{a+b}{2} \\ 1 - 2 \left( \frac{x-a}{b-a} \right)^2, a \leq x \leq \frac{a+b}{2} \\ 1, b \leq x \leq c \\ 1 - 2 \left( \frac{x-c}{d-c} \right)^2, c \leq x \leq \frac{c+d}{2} \\ 2 \left( \frac{x-d}{d-c} \right)^2, \frac{c+d}{2} \leq x \leq d \\ 0, x \geq d \end{array} \right.$$

(Equation 1)

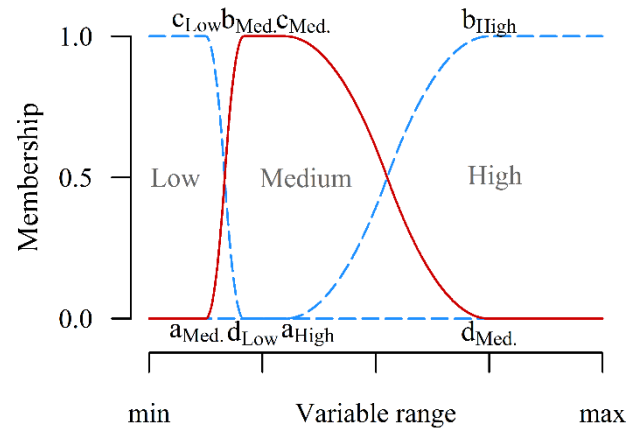


Figure 1. Parameters ( $a_m$ ,  $b_m$ ,  $c_m$  and  $d_m$ ) defining an asymmetric  $\Pi$ -membership function.

Table 1. Variables selected for the most parsimonious fuzzy rule-based system for each species, linguistic categories assigned to each fuzzy set and optimal parameters of the membership functions describing these fuzzy sets.

Species	Variable	Label	Parameters
<i>Amphilius uranoscopus</i>	Depth	Very Low	(0, 0, 0, 0.1)
		Low	(0, 0.1, 0.1, 0.79)
		High	(0.1, 0.79, 1.4, 1.4)
<i>Barbus spp.</i>	Velocity	Low	(0, 0, 0.01, 5.15)
		High	(0.01, 5.15, 7.29, 7.29)
	Depth	Very Low	(0, 0, 0, 0.1)
		Low	(0, 0.1, 0.1, 1.24)
		High	(0.1, 1.24, 1.4, 1.4)
		Substratum index	Low
High	(6.38, 8, 8, 8)		
<i>Labeo cylindricus</i>	Depth	Very Low	(0, 0, 0, 0.1)
		Low	(0, 0.1, 0.1, 1.36)
		High	(0, 1.36, 1.4, 1.4)
	Substratum index	Low	(0, 0, 4, 7.98)
High		(4, 7.98, 8, 8)	
<i>Parakneria spekii</i>	Depth	Very Low	(0, 0, 0, 0.1)
		Low	(0, 0.1, 0.1, 0.91)
		High	(0.1, 0.91, 1.4, 1.4)
	Substratum index	Low	(0, 0, 0.82, 6.65)
		High	(0.82, 6.65, 6.65, 7.80)
		High	(6.65, 7.80, 8, 8)