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Additional Information

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

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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.

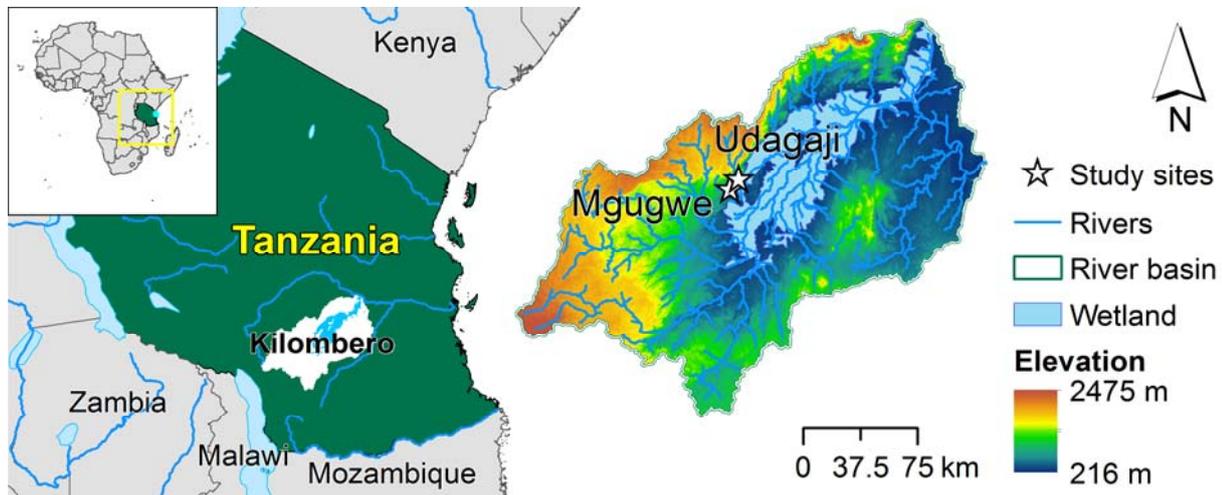
91 **2 Methods**

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 km²). In accordance, the mean annual flow of the Mgugwe River

105 corresponds to 2.83 m³/s (1957-1991) whereas that of the Udagaji River corresponds to 0.81 m³/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 ± 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 χ^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. spekkii*) 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), Π -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

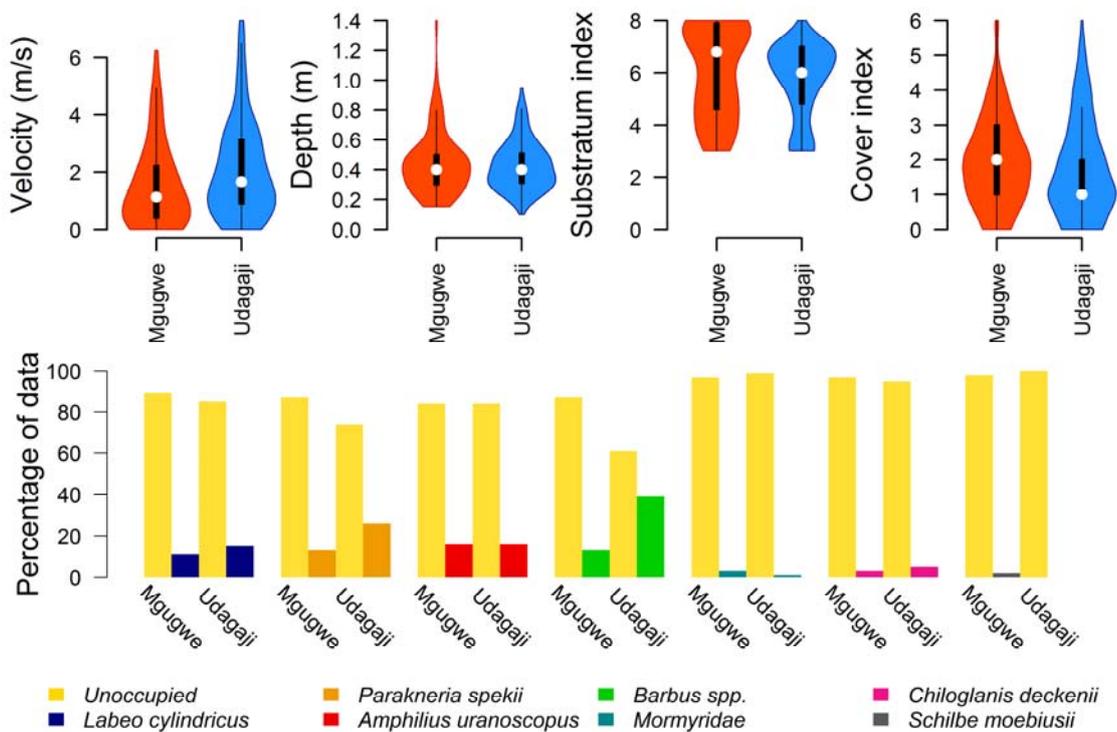
259 **3 Results**

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

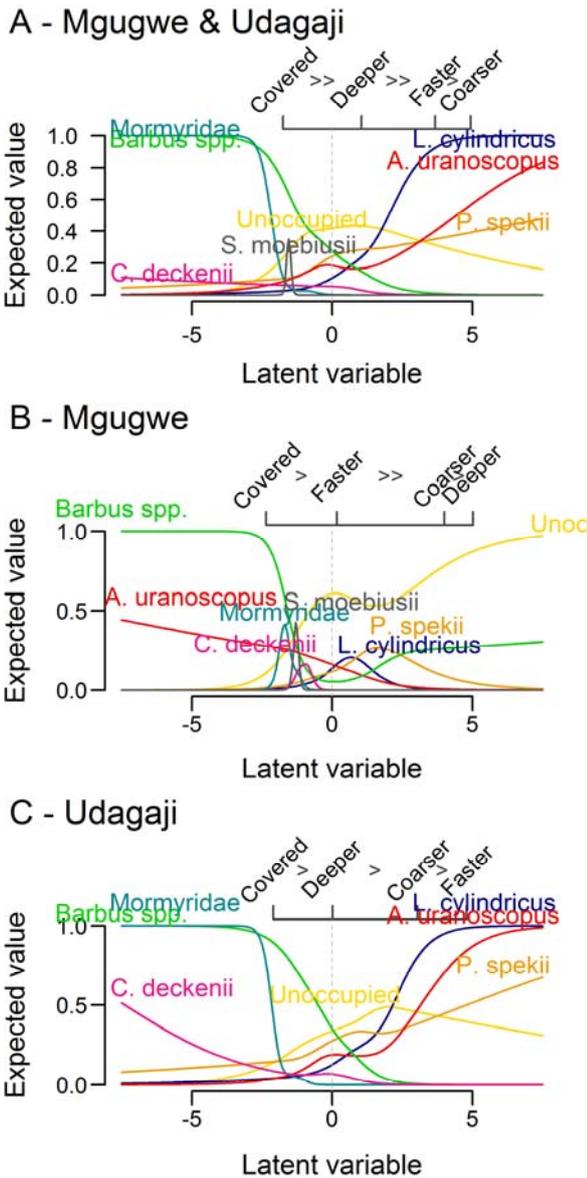
275 3.1 Assemblage preferences – Constrained Additive Ordination (CAO)

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.

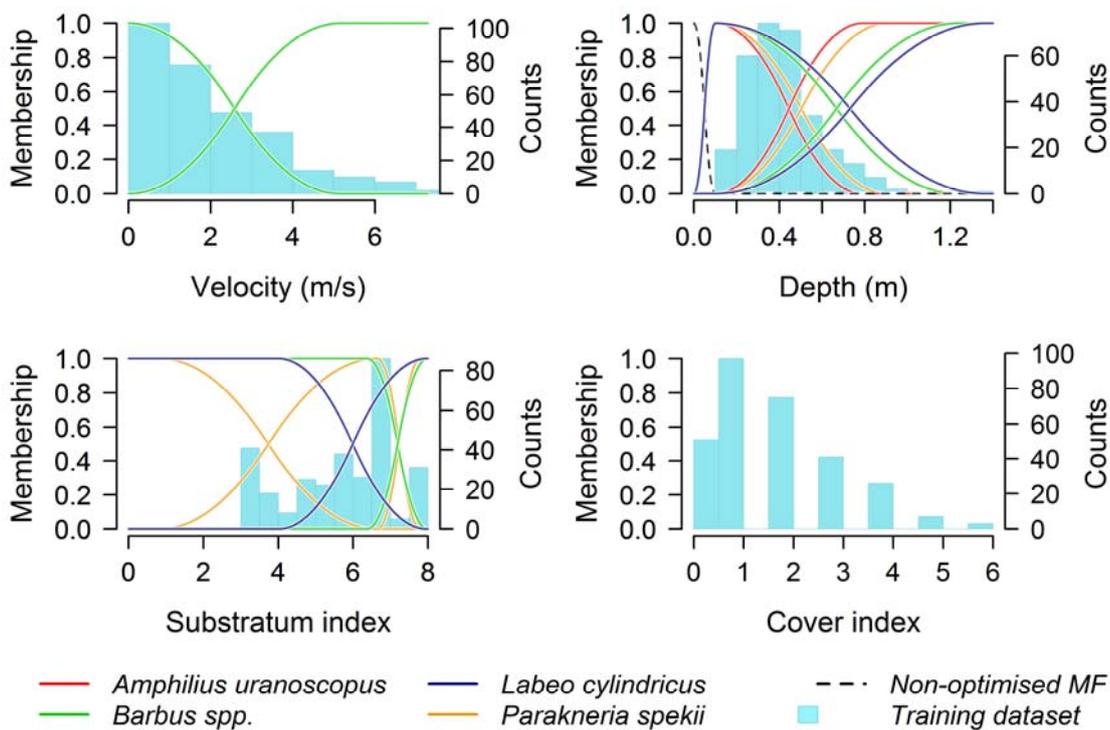
300

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).

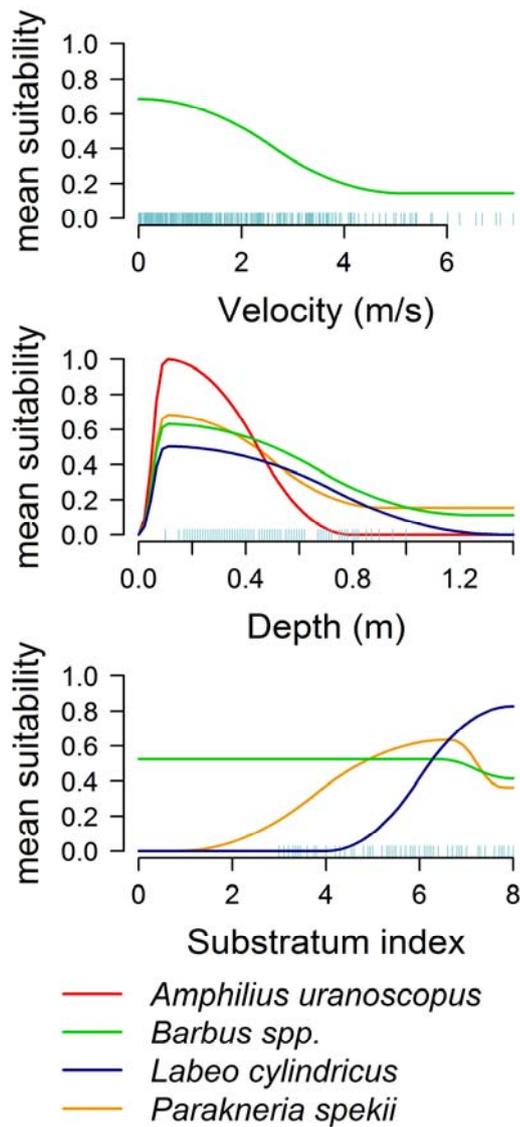
307 The best predictor variables, number of fuzzy sets (categories) and the shape of the corresponding
 308 membership functions varied among species (FIGURE 4 & TABLE 3), which indicates different
 309 environmental drivers of species presence and range of tolerance. Nevertheless, the fuzzy sets for 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.



318
 319 F I G U R E 4. Optimal number of fuzzy sets (categories) and their corresponding membership
 320 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 χ^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 χ^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 (χ^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_{presence})	Microhabitat fish occurrences (Mean number of individual)	Relevant cover (χ^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 & Minshull, 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).

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).

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 Π -membership functions (Equation 1 and Figure 1). Π -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)

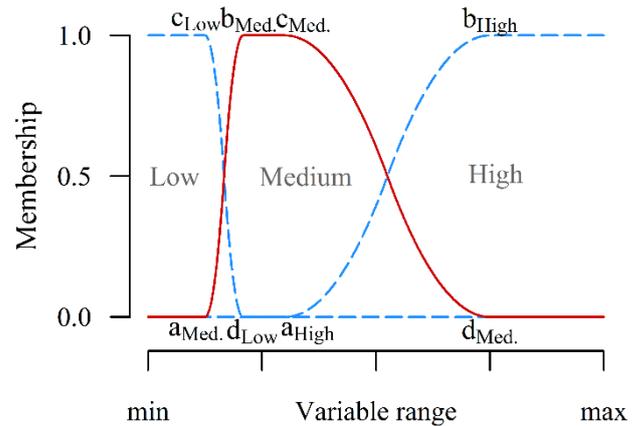


Figure 1. Parameters (a_m , b_m , c_m and d_m) defining an asymmetric Π -membership function.

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	(0, 0, 6.38, 8)
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)
		Medium	(0.82, 6.65, 6.65, 7.80)
		High	(6.65, 7.80, 8, 8)