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Structure of small tropical island freshwater fish and crustacean communities: A niche- or dispersal- based process?

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Abstract :

Determining the relative importance of niche- and dispersal-based processes in the structuring of animal communities is central in ecology. Freshwater fish and crustacean communities of small tropical islands can bring new insights for understanding these processes as all their species present a pelagic larval stage which gives them important dispersal capacities. Consequently, we hypothesized that dispersal-based process may be preponderant for structuring these communities from the regional to the local, that is, survey site, scales. Gradient forest analyses allowed us to model the effect of 12 environmental variables on freshwater taxa abundances in two southwestern Indian Ocean islands: Mayotte (26 taxa) and Reunion (21). A total of 153 surveys in Mayotte and 266 in Reunion were used for building the models. Despite the strong heterogeneity of environmental conditions between the two islands, the main factors structuring freshwater fish and crustacean communities in both islands were the elevation and the slope of the sites. The observed structure appeared more pronounced for predatory species than for primary consumers and omnivores. As predators generally have limited locomotor capacities, it is concluded that dispersal-based process structures these communities not only at large geographical scales but also at the intra-watershed scale, by limiting the inland penetration (or dispersion) of species in relation to their locomotor capacities. However, more knowledge concerning ecological traits and taxonomic status of many species is needed to confirm this assumption. Abstract in French is available with online material

Keywords : abundances, diadromy, environmental gradients, migration, taxonomic richness, western Indian Ocean

61 1. INTRODUCTION

62 Investigating the mechanisms which drive communities structure is a central task in community ecology
63 (Menge and Olson, 1990). Niche- and dispersal-based processes are among the most influential mechanisms
64 structuring animal communities. Niche-based process suggests that environmental habitat conditions and
65 biotic interactions (i.e. competition and/or predation) generate a spatial segregation of species depending on
66 their ecological requirements (Legendre et al., 2005). On the other hand, dispersal-based process advocates
67 the existence of dispersal limitations between habitat patches due to geographical or physical barriers. In
68 this context, dissimilarities in species compositions can occur between habitat patches due to speciation-
69 extinction events (Barton et al., 2013). Nevertheless, the relative importance of niche- and dispersal-based
70 processes are generally hard to disentangle, and depend on the geographic scale of the studies (Chase and
71 Myers, 2011). At large geographic scales, dispersion of propagules may play a preponderant role in
72 community structure by limiting the connectivity between populations present in distant localities (Leprieur
73 et al., 2009). Oppositely, at smaller geographic scales, niche-based processes related to biotic and abiotic
74 habitat preferences may dominate when habitat conditions strongly differ between localities. Indeed,
75 dispersal opportunities are rarely limited when localities are close to each other, but the local environmental
76 conditions may reduce the capacity of propagules to settle in new areas. Beyond the geographical scale, the
77 relative importance of niche- and dispersal-based processes are also influenced by species-specific traits
78 (Soininen, 2010). For example, some fish species have developed specific behaviors adapted to their
79 physiological and anatomical traits that allow them to pass barriers swimmers cannot get beyond (Carvajal-
80 Quintero et al., 2015; Schoenfuss and Blob 2003). Consequently, these species have enhanced active
81 dispersal abilities (Jenkins et al., 2007) which limit the importance of dispersal-based process in structuring
82 their populations.

83 While riverine fish and crustacean communities of small tropical islands remain poorly examined,
84 processes structuring these communities can bring new insights on the relative importance of niche- and
85 dispersal-based processes across nested geographic scales. Indeed, small oceanic islands are discrete

86 entities, presenting contrasted geomorphology, which are separated from continents, or other islands, by
87 variable distances (Fitzsimons et al., 2002). Within each island, the watersheds present major environmental
88 gradients. Indeed, streams flow from several thousand meters of elevation to the sea in a few kilometers
89 (Strauch et al., 2017). Consequently, very lotic- (i.e. cascades, rapids) and lentic- (i.e. pools, shoals) habitats
90 successively occur within several meters of river length. Finally, indigenous fish and crustacean species of
91 insular streams are diadromous species, or estuarine species with a strong tolerance to salinity variations
92 (Keith et al., 2006). Among the diadromous species, some are catadromous, adults reproduce in sea and
93 their juvenile grow and mature in rivers, whereas others are amphidromous, adults reproduce in rivers,
94 larvae grow in sea and juvenile return to rivers to grow and mature (McDowall, 1988). For all these species,
95 connectivity between islands, and between different watersheds within an island, mainly occurs during the
96 marine larval stage. Therefore, the occurrence of a species at a given location within a watershed first
97 depends on its capacity to disperse and reach this watershed on an island, and secondly on the presence of
98 suitable habitat conditions to settle in the newly colonized environment. Because of the marine larval phase,
99 the colonization of river systems by juveniles necessarily starts from the estuary at each generation. As a
100 result, the distribution of fish and crustacean species along the watersheds not only depends on local habitat
101 conditions but also on the capacity of individuals to reach upstream sections. The active migration from the
102 estuary thus represents a second dispersal step. This migration shapes the local distribution of species as a
103 function of rivers morphology and individuals locomotor capacities (i.e. swimming, leaping, crawling ...)
104 that allow their upstream progression. Therefore, the structure of freshwater fish and crustacean assemblages
105 in oceanic islands are expected to be controlled by successive dispersal- and niche-based processes taking
106 place at the inter-island (i.e. regional), island (i.e. inter-watershed), and watershed scales. Finally, niche-
107 based processes related to biotic and abiotic habitat conditions are probably the most influential drivers of
108 these assemblages at the local scale (i.e. river site) in small tropical islands.

109 In small tropical islands, life traits of many fish and crustacean species, particularly their trophic
110 position, are related to their dispersion capacity and habitat preferences. Indeed, spatial segregation of fish
111 and crustacean species depending on their trophic levels have been observed within watersheds (Fitzsimons

112 et al., 2002, Schoenfuss and Blob, 2007; Cooney and Kwak, 2013) as well as at the sites, or micro-habitats,
113 scales (McRae et al., 2013; Donaldson et al., 2013). Generally, species of lower trophic level tend to be able
114 to migrate higher upstream and to inhabit faster-flowing areas compared to predators. These capabilities
115 probably evolved as predation avoidance strategies (Hein and Crowl, 2010; Diamond et al., 2016; 2019).
116 Lower trophic level species, such as gobies or shrimps, tend to present better locomotor capacities compared
117 to predators (Fitzsimons et al., 1997). They can resist faster flow conditions and/or climb-up more important
118 barriers than most predator species (Blob et al., 2010; Hein and Crowl, 2010). These differences suggest
119 that the relative contribution of niche- and dispersal-based processes may differ between trophic groups due
120 to their different locomotor capacities. For example, the capacity of low trophic level species to climb-up
121 waterfalls may enhance their dispersion capacities and, consequently, reduce the importance of dispersal-
122 based process in structuring the communities observed locally.

123 In this context, the present study investigated the relative importance of niche- and dispersal-based
124 processes for explaining the structure of freshwater fish and crustacean communities of two oceanic islands,
125 Mayotte and Reunion, Indian Ocean. While the regional scale was examined qualitatively based on
126 assemblage comparisons, an extensive dataset of 153 surveys in Mayotte and 266 in Reunion was analyzed
127 to investigate processes shaping stream communities at the island, the watershed, and the site scales. More
128 particularly, we hypothesized that:

- 129 (a) at the regional scale, the importance of dispersal-based process for explaining freshwater fish and
130 crustacean species richness is promoted by extended distances between the islands;
- 131 (b) more locally, dispersal-based processes also greatly influence freshwater fish and crustacean
132 communities because the colonization occurs from the river mouths at each generation;
- 133 (c) and the relative importance of dispersal- compared to niche-based processes is greater for predators
134 compared to lower trophic groups in relation to their lower locomotor capacities.

135

136 **2. METHODS**

137 **1. Study areas and field sampling**

138 Mayotte and Reunion are two small tropical islands in the southwestern Indian Ocean (Figure 1a).
139 Indigenous fishes and crustaceans communities inhabiting freshwaters are similar with approximately 20
140 species shared between the two islands (Keith et al., 2006). In Mayotte, Eberschweiler (1987) enumerated
141 27 permanent rivers joining the sea, their watershed areas ranging from two to 23 km². In Reunion, only 13
142 permanent rivers join the sea, their watershed areas ranging from 28 to 154 km² (Robert, 1986).

143 A total of 86 and 61 sites were sampled from 2004 to 2017 along the downstream-upstream gradient
144 of the main rivers of Mayotte (Figure 1b) and Reunion (Figure 1c), respectively. In Mayotte, sampling was
145 repeated between one and seven years at each site (Figure 1b). As a result, 161 surveys were conducted with
146 12 to 23 surveys each year from 2008 to 2012, in 2014, 2015 and 2017, six in 2013 and 40 in 2016. In
147 Reunion sampling was performed from one to 12 different years at each site (Figure 1c) resulting in 366
148 surveys (i.e. 29 to 35 surveys each year from 2004 to 2014, four in 2015 and 22 in 2016).

149 Fish and crustaceans were sampled using a portable electro-shocker (Deka, 3000 or Hans Grassl,
150 IG 200). The sampled river length was at least ten time the mean river width. The upstream and downstream
151 limits of the sites were blocked by a net or a physical barrier (i.e. waterfall, weir ...) to limit fish and
152 crustacean emigration and immigration. To ensure sampling effectiveness and representativeness, two
153 sampling procedures were applied depending on the river width (Olivier et al., 2004). When the river width
154 was less than five meters, the whole area of the river site was prospected by fishermen moving upstream
155 (i.e. complete sampling). When the river width was greater than five meters, the sampling was stratified by
156 hydromorphic units (i.e. cascade, rapid, riffle, run, shoal and pool). In this case, the hydromorphic units
157 were firstly identified based on mean water velocity and depth following Malavoi and Souchon (2002), and
158 their surfaces were estimated using a laser meter (Leica DISTO D5). Then several sampling units ranging
159 from 10 to 25 m² were distributed within each hydromorphic unit proportionally to its surface, ensuring that
160 a minimum of 200 m² was sampled across the whole site. Finally, each sampling unit was prospected by
161 moving upstream using the electro-shocker. For both sampling procedures, fish and crustacean were

162 captured by a minimum of three operators equipped with hand nets (width 50 cm, maximum mesh
163 size four mm) and positioned immediately downstream to the operator manipulating the electro-shocker.

164

165 **2. Estimate of taxa abundances**

166 Captured fish and crustaceans were identified at the species level using the identification keys provided by
167 Keith et al. (2006) except individuals for which identification to the species level is doubtful: small-sized
168 *Eleotris* and *Anguilla* spp., all specimens of the *Ambassis*, *Glossogobius*, *Kuhlia* and *Microphis* genus, as
169 well as Carangidae and Mugilidae. Each taxon was assigned to one of three different trophic levels (i.e.
170 primary consumers, omnivores and predators) based on published data (Table S1). For simplification
171 purpose, herbivorous and saprophagous species were considered as primary consumers when insectivorous
172 and piscivorous species were considered as predators.

173 The abundance of each taxon was estimated based on capture per effort units (CPUE, ind.m⁻²) whatever the
174 fishing procedures. For the complete sampling procedure, the abundance of one taxon was the number of
175 individuals divided by the fished area (m²). For the stratified sampling procedure, the abundance of each
176 taxon was first calculated within each hydromorphic unit by averaging the number of individuals captured
177 in each sampling unit divided by its area. Then, the abundance of one taxon in a sampling site was obtained
178 by the mean of the abundance in all hydromorphic units weighted by their relative surface proportion in the
179 river site. Non-natives species were not considered in the analyses as their abundance in a given site depends
180 both on ecological process and on (re)stocking events.

181

182 **3. Environmental descriptors**

183 A total of 17 environmental variables describing the river sites from the island to the site scale were either
184 recorded in the field or estimated based on GIS data (Table 1). Ten environmental factors reflecting local
185 physicochemical conditions and habitat characteristics were measured during each survey. The local
186 physicochemical conditions were the water temperature (°C), pH, conductivity (μS.cm⁻¹) and the dissolved
187 oxygen (O₂, mg.l⁻¹) measured using a multi-parametric probe (YSI, Professional Plus). The local habitat

188 conditions were described as the relative proportion of hydromorphic units in the site. Six environmental
189 variables describing the location and accessibility of each site at the watershed scale were recorded. The
190 GPS coordinates of river site were used to determine: the distance from the river mouth (km), the elevation
191 (m) and the slope (%), i.e. the difference between the altitude of the lower and upper limits of the site divided
192 by its length (m). Three descriptors were used to reflect the accessibility of each site from the estuary: the
193 number, the maximum height (m) and the cumulative height (m) of migration barriers such as waterfalls,
194 dams, weirs, etc. located downstream. The location and height of migration barriers were based on previous
195 studies (DEAL, 2011, 2017) complemented by field observations. Finally, the length of the main river (km)
196 within each watershed was estimated using GIS. All GIS analyses were made with the open source
197 Qgis v.2.18.6 software (QGIS Development Team, 2017).

198

199 **4. Data analyses**

200 In order to identify redundant parameters, a correlation analysis of all environmental variables was
201 performed based on the Kendal correlation coefficient (τ). When τ value between two or more parameters
202 was greater than 0.70, only one parameter was included in the following analyses. The selected parameter
203 was either the one providing the strongest effect on species abundances based on visual inspection of
204 univariate plots, or the parameter that best summarized the others. The distance from the river mouth was
205 correlated with elevation in Reunion ($\tau = 0.74$) and the number, the maximum height and the cumulative
206 height of migration barriers were inter-correlated for the two islands ($\tau \geq 0.78$). The elevation was kept for
207 the subsequent analyses as it showed a greater influence on species abundances variation than distance from
208 the river mouth. The cumulative migration barriers height was also kept as it synthetizes the number of
209 migration barriers and their maximum height. In addition, the water temperature and pH were removed from
210 subsequent analysis as the water temperature is higher in Mayotte's rivers due to the proximity of the island
211 to the equator and because pH values were missing in approximately 30% of the Reunionese dataset.
212 Consequently, further analyses were performed on a total of 12 environmental variables: eight collected at
213 the site scale (i.e. the percentages of cascades, rapids, riffles, runs, shoals and pools in the river site, along

214 with conductivity and dissolved oxygen concentration), three representing the watershed scale (i.e. the site
215 elevation and slope and the cumulative migration barriers height) and one, the main river length,
216 representing the island scale.

217

218 In a first step, the habitat conditions were compared between the two islands using a between class
219 PCA of environmental variables based on sites. This between class PCA was useful to limit the influence
220 of the sites sampled several times compared to the sites sampled only once (Dolédéc and Chessel, 1987).
221 Then, the way environmental variables influence the structure of freshwater fish and crustacean
222 communities was investigated using gradient forest analyses (GF, Ellis et al., 2012) for each island
223 separately. GF is a multivariate analysis that comprises two main steps. The first one consists in modeling
224 how the abundance of each taxon vary in response to environmental variables using random forest models
225 (RF, Breiman, 2001). During a second step, the RF models obtained for each taxon are aggregated in order
226 to calculate the overall importance of each environmental variable. The importance of environmental
227 variables and the performance of RF for each species are thus ranked based on their aggregated goodness
228 of fit values (pseudo-R²). As GF analyses are based on RF models, GF inherits the main advantages of RF
229 which are: to not depend on the normality or homoscedasticity of the data, to not require transformation of
230 the data, and to integrate nonlinear responses (Pitcher et al., 2012). This latter advantage appeared
231 particularly relevant in the context of our study as data preview revealed non-linear relationships between
232 taxa abundances and several environmental variables. To limit the bias caused by rare species, GF analyses
233 were performed on species occurring in more than 3.5% of the surveys only (Roubeix et al., 2017).

234

235 Finally, the changes in abundances of primary consumers, omnivores and predators along
236 environmental gradients were modeled to describe how trophic groups shape fish and crustacean
237 communities' structures in the two islands. In this purpose, RF models were adjusted with primary
238 consumers, omnivores or predators' abundances as response variables, whereas the same environmental
239 gradients as in GF analyses were used as explanatory variables. The importance of each variable was

240 assessed based on the node purity index (Banerjee et al., 2019). For each variable, the significance of the
241 node purity index was estimated by comparing the predicted values to a null distribution obtained with 1000
242 random permutations of the values. A significant decrease of the node purity index is interpreted as an
243 information gain associated with the variable compared to the null distribution (Archer, 2016).

244
245 Statistical analyses were performed with the open source R v.3.3.1 software (R Development Core
246 Team, 2016) implemented with the packages *ade4* (Dray and Dufour, 2007) for PCA analyses,
247 *gradientForest* (Ellis et al., 2012) for GF analyses, *randomForest* (Liaw and Wiener, 2002) and *rfPermute*
248 (Archer, 2016) for RF analyses.

249

250 **3. RESULTS**

251 **1. Environmental dissimilarities between islands**

252 Due to missing data, the between-sites PCA was performed on 12 environmental variables and 153 surveys
253 in Mayotte and 262 in Reunion (Figure 2). Globally, the sites of Mayotte and Reunion were well
254 discriminated along the first PCA axis, and only slightly along the second and the third axis, which
255 represented 34%, 18% and 12% of the total inertia, respectively. The first axis of the PCA was mainly
256 associated with the conductivity, the percentage of shoals and the main river length (Figure 2a-b). The
257 second axis of the PCA was mainly related to the slope of the sites and their elevation (Figure 2a), whereas
258 the third axis was chiefly related to the cumulative height of migration barriers located downstream to the
259 site (Figure 2b).

260 In Mayotte, the sites were characterized by higher proportions of shoals (i.e. lentic and shallow
261 hydromorphic units), higher conductivity, and lower dissolved oxygen compared to Reunionese sites
262 (Table 1). Within each watershed, the sites sampled in Mayotte were generally located at a lower elevation
263 with a lower cumulative height of the downstream barriers compared to Reunionese sites. Finally, in
264 Mayotte the main river lengths were shorter.

265

266 **2. Fish and crustacean communities**

267 A total of 39 indigenous fish and crustacean taxa were captured in Mayotte (Figure 3a), among them 26
268 (67% of the total) were diadromous and 13 (33%) were marine and estuarine (Table S1). Thirteen taxa were
269 observed in less than 3.5% of the surveys (Figure 3a) and were thus excluded from the following analyses.
270 In Reunion, all the 21 taxa captured (100%) were diadromous (Figure 3b, Table S1). All these taxa were
271 present in more than 3.5% of the surveys (Figure 3b). The most abundant fish and crustacean species in
272 Mayotte were *Anguilla marmorata* and *Eleotris klunzingerii*, *Caridina longirostris* and *C. typus*,
273 respectively (Figure 3c) while in Reunion they were *Sicyopterus lagocephalus* and *Cotylopus acutipinnis*,
274 *Atyoida serrata* and *Macrobrachium australe*, respectively (Figure 3d).

275

276 **3. Importance of environmental variables**

277 The response of the taxa abundances to 12 environmental variables was modelled using two separate GF:
278 one for 26 taxa in Mayotte, and one for 21 taxa in Reunion. A total of 153 surveys in Mayotte, and 262 in
279 Reunion, were included in these analyses due to missing data. The average R^2 was 0.19 in Mayotte and 0.28
280 in Reunion which means that the variance in species abundances was moderately explained by
281 environmental variables in both islands (Roubeix et al., 2017). The four taxa for which the total deviance
282 was best explained by GF were *Ophieleotris cf. aporos*, *A. marmorata*, *Glossogobius* spp. and *Eleotris*
283 *mauritiana* in Mayotte (Figure 4a), *E. klunzingerii*, *A. marmorata*, *M. australe* and *C. acutipinnis* in Reunion
284 (Figure 4b). In both islands, freshwater fish and crustacean communities were mostly structured along the
285 elevation and slope gradients (Figure 5a-b), which represent the watershed scale. However, in Mayotte the
286 relative importance of slope for structuring freshwater fish and crustacean communities was much lower
287 than the relative importance of the elevation (Figure 5a).

288

289 **4. Response of primary consumers, omnivores and predators**

290 The RF describing the response of primary consumers and omnivores to environmental gradients explained
291 only 6% and 1% of the variance of primary consumers and omnivores abundance in Mayotte versus 42%

292 and 43 % in Reunion, respectively. The RF describing the response of predators to environmental gradients
293 were well adjusted for both islands with 51% of the variance of predators' abundance explained in Mayotte
294 and 64% in Reunion. In Mayotte, the abundances of primary consumers and omnivores were not
295 significantly associated with all the explanatory variables (Table S2, Figure 6a-c-e-g, $P \geq 0.05$). By contrast,
296 the abundances of primary consumer and omnivores were significantly explained by the elevation, the slope,
297 the cumulative migration barriers height and the main river length in the watershed in Reunion (Table S2,
298 $P \leq 0.02$). More precisely, the abundance of primary consumers decreased when elevation and slope
299 increased (Figure 6b-d). The peak observed for a slope of approx. 3% is probably an artefact related to the
300 high abundances recorded in one single site with a 3% slope but sampled during 11 different years. The
301 elevated abundance of primary consumers at this site can be explained by the presence of an intermittent
302 river section immediately upstream. Consequently, when the section becomes dry, migrating juveniles are
303 blocked and their abundance at the sampling site increases. The abundance of omnivores globally decreases
304 when elevation and slope increased (Figure 6f-h). The abundance of predators was significantly related to
305 the elevation of the site, its slope, the cumulative migration barriers height downstream to the site and the
306 length of the main river of the watershed in Mayotte and Reunion (Table S2, $P \leq 0.01$). In both islands,
307 predators' abundance decreased when elevation and slope increased (Figure 6i-j-k-l).

308

309 **4. DISCUSSION**

310 **1. Taxa richness in Mayotte and Reunion**

311 At a regional scale, species richness is generally structured by dispersal-based process limiting the
312 connectivity between habitat patches (Henriques et al., 2017). The effects of dispersal-based processes are
313 expected to be more important in the context of small oceanic islands where freshwater habitats consist in
314 discrete patches, distant from each other. However, although dispersal-based processes are supposed to be
315 dominant, our findings suggest that the difference of fish and crustacean taxonomic richness between
316 Mayotte (39 taxa) and Reunion (21 taxa) likely results from a combination of both dispersal- and niche-
317 based processes. Indeed, the difference in diadromous fish and crustacean richness between the two islands

318 appeared primarily explained by dispersal limitation, whereas changes in marine and estuarine taxa are
319 probably more related to niche-based process.

320 Diadromous taxa correspond to 67% of the total in Mayotte, and 100% in Reunion, indicating they
321 play a crucial role for structuring the fish and crustacean communities of these islands. The higher taxonomic
322 richness of diadromous taxa recorded in Mayotte can be explained by the proximity to Madagascar and the
323 African continent (300 km compared to 700 km for Reunion). Indeed, due to the general oceanic circulation
324 and distances between sites, the pelagic stage of fish larvae should connect more easily between Mayotte
325 and Madagascar, or east Africa, than between the later localities and Reunion (Crochelet et al., 2016). This
326 hypothesis is supported by the presence of several diadromous species observed in Mayotte during our study
327 such as *Redigobius bikolanus*, *Hypseleotris cyprinoides* and *Ophiocara porocephala* which are also present
328 in Madagascar (Fricke et al., 2018) or *R. bikolanus* present in South Africa (Whitfield, 1994). All these
329 species are not present in Reunion.

330 In contrast, dispersal-based processes at the regional scale appeared less important for explaining
331 that 13 marine and estuarine taxa were observed in Mayotte but not in Reunion. This difference in the
332 number of marine and estuarine taxa can be explained by the higher proportion of sites with low elevation
333 (i.e. between 0 and 5 meters a.s.l), and the higher amplitude of tides, in Mayotte compared to Reunion. High
334 tide amplitude probably allows marine and estuarine taxa to progress inland more easily and to reach the
335 downstream sites surveyed in this study. Indeed, numerous marine and estuarine taxa recorded in Mayotte
336 downstream sites, such as *Megalops cyprinoides*, *Kuhlia caudavittata*, *Lutjanus argentimaculatus* and
337 *Ambassis* spp., are also frequently observed in coastal waters of Reunion (Fricke et al., 2009). These species
338 do occur at proximity to the Reunionese rivers but their absence in downstream riverine habitats is probably
339 related to the lack of suitable local environmental conditions, particularly the low proportion of lentic areas.
340 The absence of marine and estuarine taxa in downstream Reunionese sites is thus better explained by niche-
341 based processes. However, these comparisons of taxonomic richness between the two islands should be
342 considered carefully. Indeed, the taxonomic status of many of these species are still discussed and may be
343 reevaluated in the future. For example, using molecular analyses of COI gene, Mennesson and Keith (2017)

344 demonstrated that *Eleotris fusca* was not a unique species distributed in the Indo-Pacific area, but a complex
345 of two species: one, *E. fusca*, being restricted to the Pacific Ocean, the other one, *E. klunzingerii*, observed
346 in the Indian Ocean only.

347

348 **2. Process structuring freshwater communities from island to site scales**

349 From the island to the site scales, the distance separating distinct habitat patches is usually not greater than
350 a few kilometers. In such a situation, the relative importance of dispersal-based process is expected to be
351 reduced in favor to niche-based process (Henriques et al., 2017). However, this hypothesis was not fully
352 supported for freshwater fish and crustacean communities in Mayotte and Reunion. Indeed, our results
353 suggested that freshwater communities are primarily influenced by factors associated with dispersal-based
354 process at the watershed scale. Despite obvious differences in environmental conditions between the two
355 islands, the communities are mainly structured by the same abiotic variables, i.e. the elevation and the slope
356 of the site. This pattern was similar in both islands although rivers in Mayotte are shorter with more lentic
357 habitats compared to those in Reunion. The elevation of a site and, to a lesser extent its slope, are two
358 variables reflecting its position within a watershed. These abiotic variables are thus closely related to
359 dispersal constraints that may limit accessibility to upper river sites for the juveniles of most species.
360 Accordingly, individuals, and thus species, with lesser locomotor abilities are not able to cross the river sites
361 presenting strong water velocities, and/or the most downstream migration barriers. The sites featured by
362 high water velocities are associated with steep hydromorphic units (i.e. rapid, cascade) which occur more
363 frequently when the slope of the river increases (Malavoi and Souchon, 2002). Therefore, the more upstream
364 is a site, the more likely individuals observed there have been obliged to cross physical barriers when
365 migrating from the river mouth.

366

367 **3. Functional groups contribution to communities' structure**

368 Taxa intrinsic characteristics, such as their trophic position or maximal body size, are known to influence
369 communities as they relate to their dispersal capacities and/or habitat preferences (Soininen, 2010). This

370 hypothesis was supported by our results as the effects of elevation and slope on the variation of predatory
371 species abundances were highly significant and RF models explained more than 50% of the deviance in
372 both islands. By contrast, primary consumers and omnivores abundances responded moderately to these
373 gradients in Reunion (approx. 40% of the deviance explained by RF model) and did not respond significantly
374 to the same gradients in Mayotte (less than 6% of the deviance explained by RF model). Such differences
375 can be explained by the limited locomotor, and thus dispersal, capacities of predators compared to primary
376 consumers and omnivores (Cooney and Kwak, 2013). For example, the eleotrids, which are among the most
377 abundant predatory species in the studied rivers, present poor swimming performances. Fitzsimons et al.
378 (1997) demonstrated experimentally that the Hawaiian *Eleotris sandwicensis* could not resist to flows
379 greater than 20 cm.s⁻¹. By contrast, sympatric species of the primary consumer Sicydiinae gobies can resist
380 to velocities as elevated as 100 cm.s⁻¹ (Fitzsimons et al., 1997) using their pelvic sucker to attach the
381 substrate (Maie et al., 2012). The strong locomotor capacities of Sicydiinae allows them to pass migration
382 barriers tens of meters high, or areas of very high water velocities (Schoenfuss et al., 2013). Similar
383 observations were made by Fièvet (1999) in Guadeloupe concerning two Atyidae species, *Xiphocaris*
384 *elongata* and *Atya innocus* and one Palaemonidae, *Macrobrachium faustinum*, and by Schoenfuss and Blob
385 (2003) in Hawaii concerning *Awaous guamensis*. The strong locomotor capacities of Sicydiinae, Atyidae,
386 Palaemonidae and *Awaous* spp., which are the more abundant species of primary consumers and omnivores
387 in Mayotte and Reunion, can probably explain the lower variation of abundance of these trophic groups
388 along environmental gradients.

389 To definitely conclude on the relative importance of dispersal- and niche-based processes for
390 shaping freshwater communities of small tropical islands, accurate descriptions of habitat preferences of
391 each fish and crustacean species are required. Even if dispersal-based processes appeared preponderant in
392 structuring predators along environmental gradients, it could also be possible that some individuals reach
393 upstream sites but cannot settle there because suitable habitats are lacking. Indeed, micro-habitat preferences
394 of predatory species are still largely unknown in small tropical islands. For primary consumers and
395 omnivores, previous studies demonstrated that micro-habitat conditions (e.g. water depth or flow velocity)

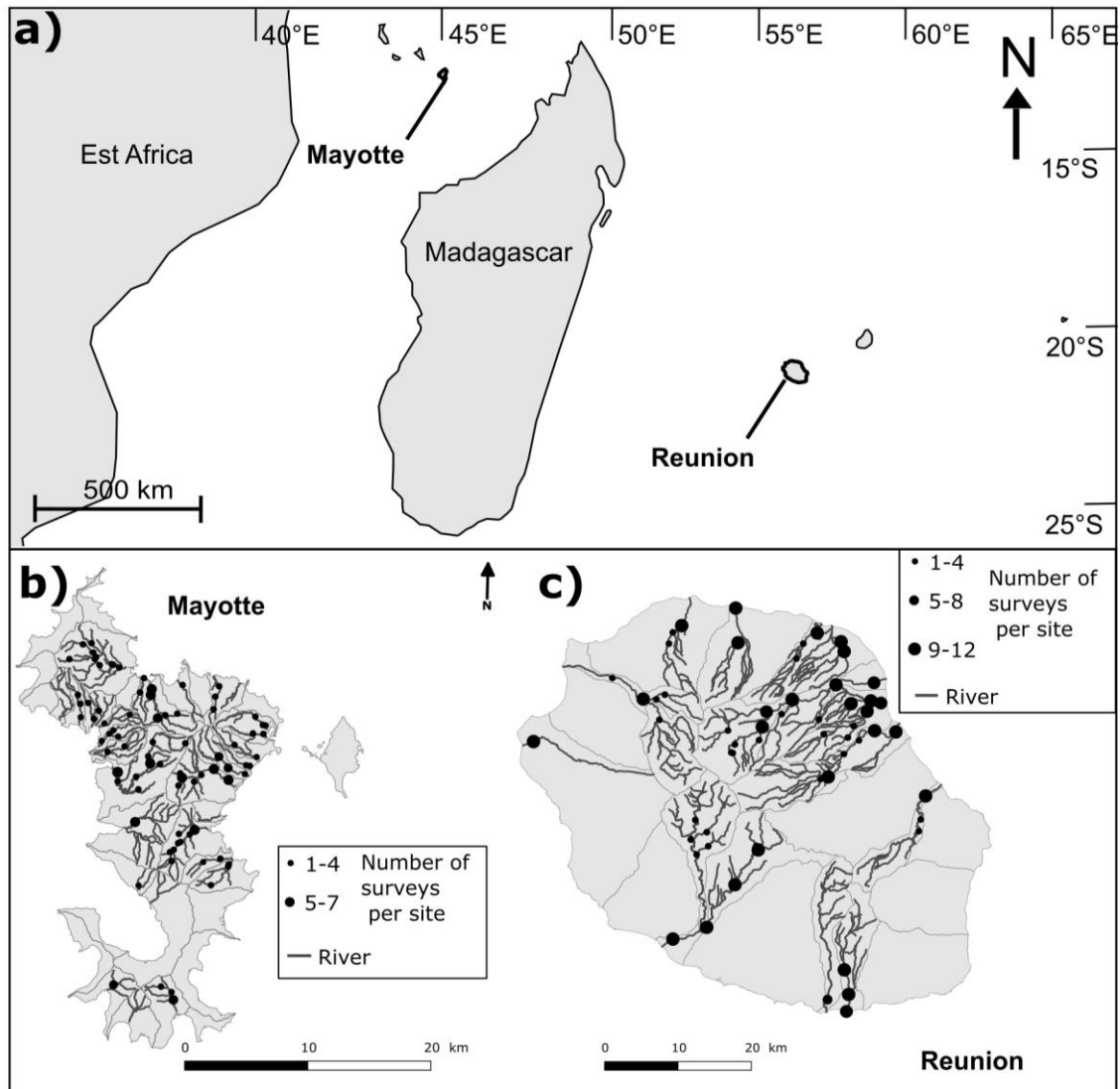
396 have a limited importance for explaining the repartition of Sicydiinae, Atyidae and Palaemonidae (Girard
397 et al., 2014; Teichert et al., 2014). Our results are consistent with these findings as primary consumer and
398 omnivores communities did not appear significantly structured by site environmental variables (i.e.
399 temperature, conductivity, percentage of hydromorphic units...). However, a stronger variation of
400 abundance of these two trophic groups along elevation and slope gradients would have been expected if
401 dispersal-based process shapes their distribution. Indeed, inter-individual difference in locomotor
402 performances can limit species abundances in upstream sites with only the most performant individuals
403 being able to reach these sites (Lagarde et al. 2018, 2020). In this context, other environmental factors such
404 as the availability of food resources (Julius et al., 2005), prey/predators or competitive interactions (Monti
405 and Legendre, 2009), can be more essential for shaping primary consumers and omnivores communities. If
406 this hypothesis is true, the structure of these communities could differ between the two islands. Further
407 studies are required to disentangle the effect of food availability, prey/predator and competitive interactions
408 on primary consumers and omnivores abundances, and definitely conclude on the relative importance of
409 dispersal- and niche-based processes in structuring these functional groups.

410 **TABLES**

411 Table 1: Median and range of values for the environmental variables recorded in Mayotte and Reunion islands at the scale of sampling sites,
 412 watersheds and islands. With N: number of sampling sites and surveys (in bracket) for which the information was available. The geographic scale
 413 at which environmental variables were compared is specified in the last column.

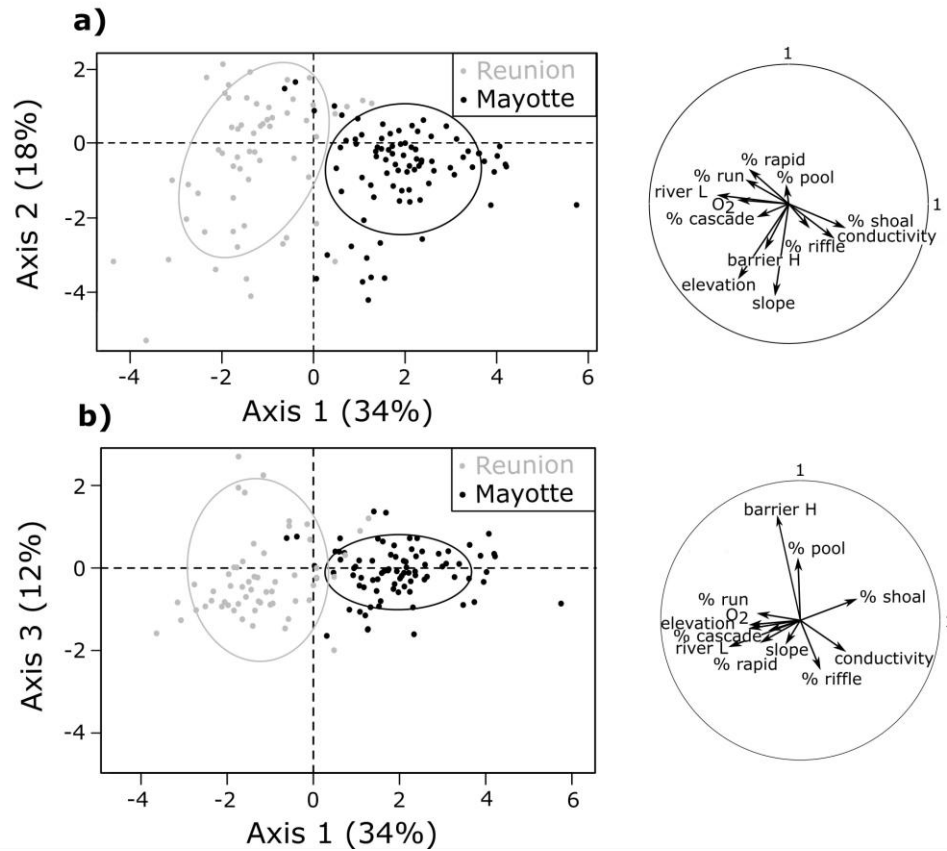
Environmental variable	Abbreviation	Mayotte			Reunion			Study scale
		N	Median	Range	N	Median	Range	
Percentage of cascades	% cascade	86 (155)	0	0-44.5	61 (365)	7.3	0-84.0	Site
Percentage of rapids	% rapid	86 (155)	0	0-54.5	61 (365)	10.2	0-75.4	
Percentage of riffles	% riffle	86 (155)	33.1	0-100	61 (365)	22.5	0-100	
Percentage of runs	% run	86 (155)	0	0-100	61 (365)	23.3	0-83.5	
Percentage of shoals	% shoal	86 (155)	50.7	0-100	61 (365)	9.7	0-94.7	
Percentage of pools	% pool	86 (155)	0	0-68.8	61 (365)	7.7	0-85.0	
Temperature (°C)	-	86 (161)	24.3	20-30.7	61 (328)	19.0	13.6-29.5	
pH	-	79 (153)	7.7	5.9-9.6	61 (261)	7.9	6.0-10.0	
Conductivity (µS.cm ⁻¹)	conductivity	85 (160)	231.0	85.0-1199	60 (355)	113.1	25.0-696	
O ₂ (mg.l ⁻¹)	O ₂	86 (161)	7.3	1.0-12.6	59 (267)	9.0	3-12	
Elevation (m)	elevation	86 (161)	47.1	2-220	61 (366)	225.0	5-890	Watershed
Distance from river mouth (km)	-	86 (161)	2.2	0.1-13.9	61 (366)	9.4	0.1-30.5	
Slope (%)	slope	86 (161)	3.1	0.4-16	61 (366)	2.7	0.2-13.1	
Number of migration barriers	-	86 (161)	1.0	0-9	61 (366)	2.0	0-11	
Migration barriers maximum height (m)	-	86 (161)	0.8	0-27	61 (366)	5.0	0-200	
Migration barriers cumulative height (m)	barrier H	86 (161)	1.5	0-29	61 (366)	6.3	0-332	Island
Main river length (km)	river L	86 (161)	6.7	2.4-19.7	61 (366)	31.0	14.0-35.0	

414



416
 417 Figure 1: Localization of Mayotte and Reunion islands in the southwestern Indian Ocean (a), and of the
 418 sampling sites within the watersheds in Mayotte (b) and Reunion islands (c). The number of surveys is
 419 indicated for each site.

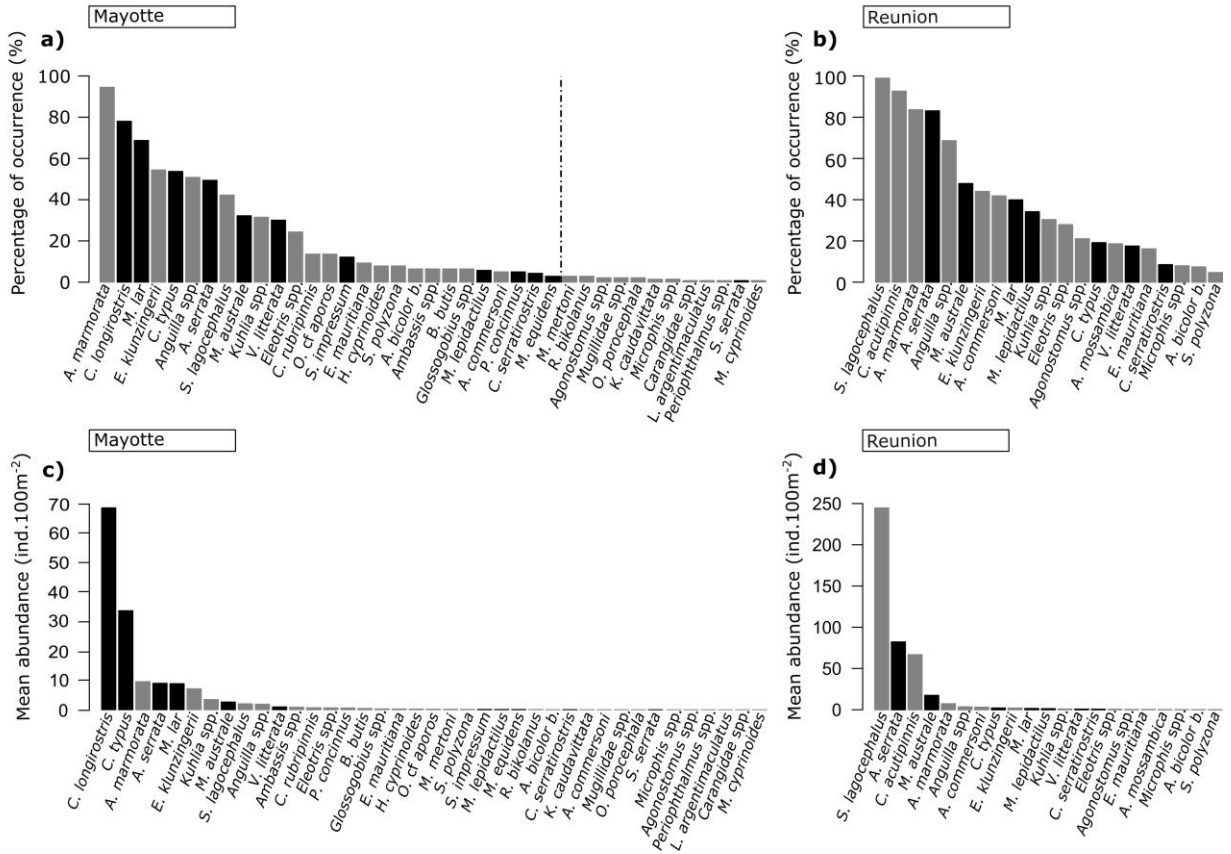
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421

422 Figure 2: First two factorial plans (**a**, **b**) of a between sites PCA describing environmental factors recorded
 423 at each site in Mayotte (black) and Reunion (grey) islands with 90% confidence ellipses. The contribution
 424 of environmental factors is presented by the correlations circles. See table 1 for the complete name of the
 425 abbreviated environmental factors.

426



427

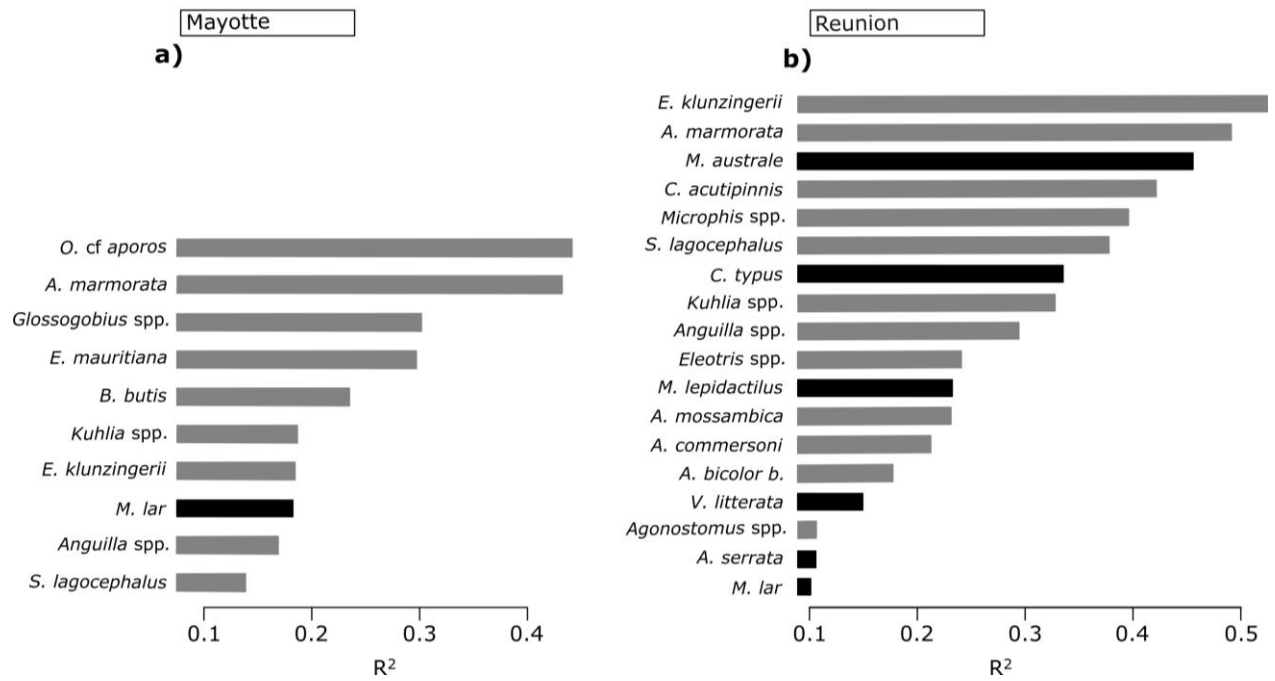
428 Figure 3: Percentage of occurrence (a, b) and mean abundance (c, d) of freshwater indigenous fish (grey

429 bars) and crustacean (black bars) taxa captured in all sites in Mayotte (a, c) and Reunion (b, d) islands.

430 The dash line delimits species for which the percentage of presence is lower than 3.5%. See table S1 for

431 the complete name of the taxa and their systematic position.

432



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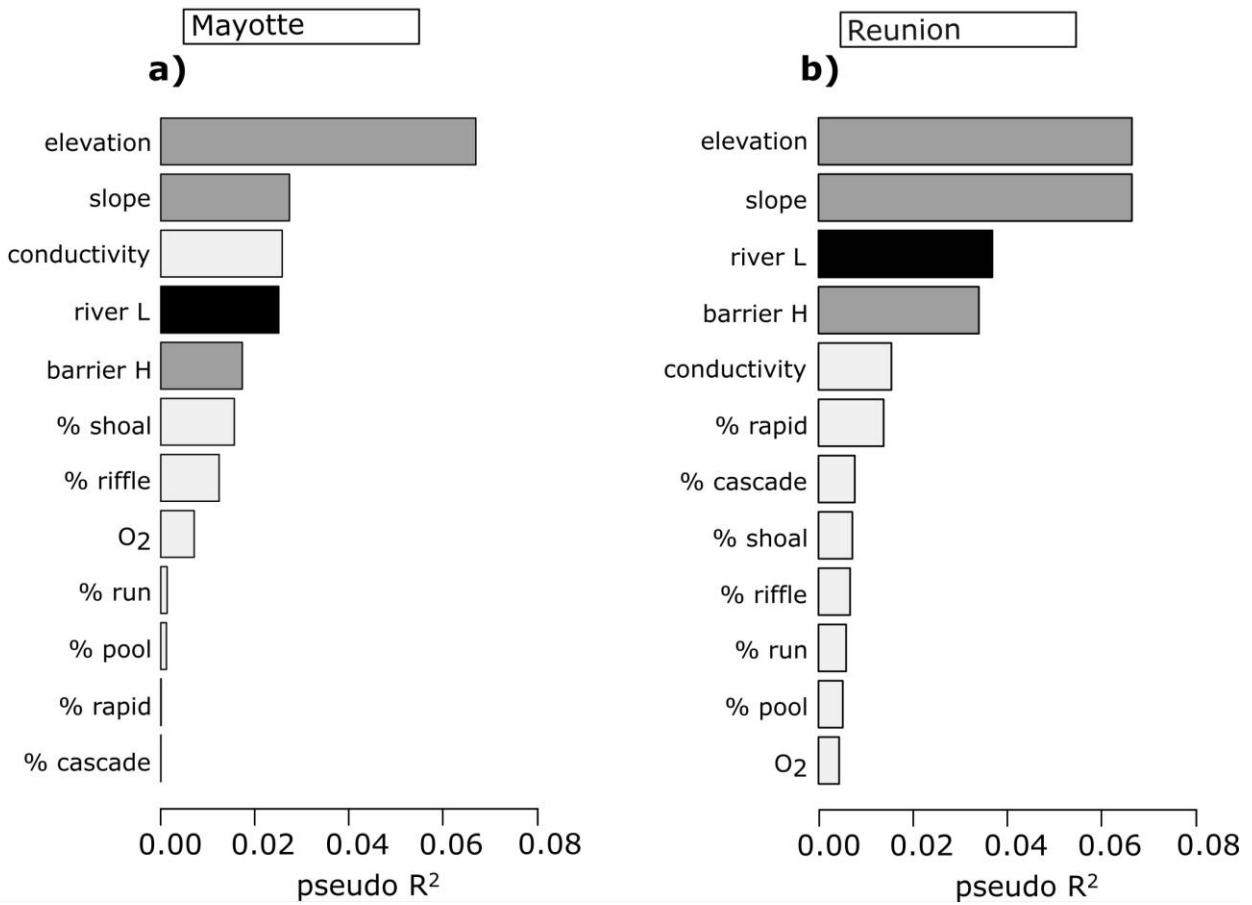
434 Figure 4: Ranking of fish and crustacean taxa structuring communities based of the pseudo R² values for

435 Mayotte (a) and Reunion (b) islands. Only taxa for which the R² value was superior to 0.1 are represented.

436 The grey bars represent fish taxa when the black bars represent crustacean taxa. For the complete name of

437 the taxa refer to table S1.

438



439

440 Figure 5: Ranking of environmental variables structuring fish and crustacean communities based of the

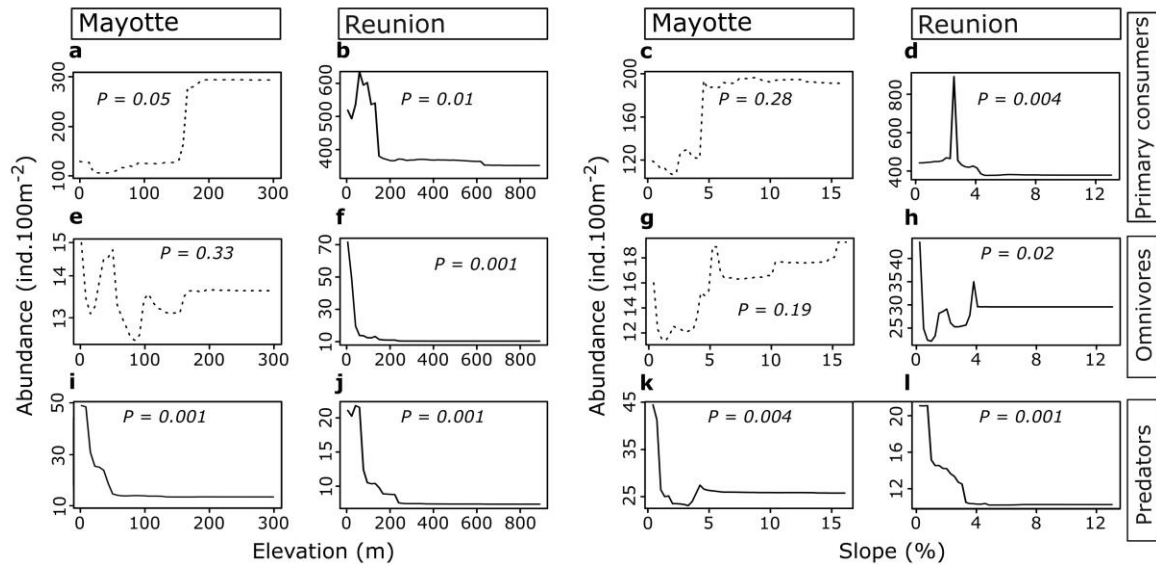
441 pseudo R² values of gradient forest analyses performed separately for Mayotte (a) and Reunion (b)

442 islands. The light grey bars correspond to variables considered at the site scale, grey bars to variables

443 considered at the watershed scale, and black bars to variables considered at the island scale. See table 1 for

444 the complete name of the abbreviated environmental factors.

445



446
 447 Figure 6: Partial response plots of primary consumers (a to d) omnivores (e to h) and predators (i to l) taxa
 448 abundances along elevation (a-b-e-f-i-j) and slope (c-d-g-h-k-l) gradients in Mayotte and Reunion islands
 449 based on random forest analyses. The p-value associated with each response was evaluated with the node
 450 purity index. Full lines represent significant responses ($P < 0.05$) when dashed lines represent non-
 451 significant responses ($P \geq 0.05$).

452
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454
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465 **Data availability statement**

466 Survey data cannot be made public for legal reasons but they are available upon request from the authors
467 and data producers

468 **Authors contribution statement**

469 RL, NT, PV and DP conceived and designed the study. PV, RL and NT performed the field work. RL, NT
470 and DP analyzed the data. RL wrote the manuscript; other authors provided editorial advice

471 **Conflict of interest**

472 The authors declare that they have no conflict of interest.

473 **Ethical guidelines**

474 All applicable regional and/or national guidelines for the care and use of animals were followed

475

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