



1 **Heterogeneity of tropical diversity and ecosystems: reefal meiofaunas in equatorial**
2 **western and eastern African islands**

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14

15 **Abstract**

16 From an ecological perspective, oceanic islands are unique marine environments that foster
17 endemic species and also facilitate dispersal as steppingstones, yet they are often understudied
18 and considered missing pieces in large-scale biological patterns. In this study, we focused on
19 ostracods and foraminifera as two representative meiobenthic groups from the São Tomé-
20 Príncipe (STP) Archipelago in tropical east Atlantic and the Zanzibar Archipelago in west
21 Indian Ocean. We scrutinized the diversity distribution and faunal structure of these two island
22 regions in similar climatic and oceanographic settings in different biogeographic provinces. We
23 found that the STP is of much lower diversity compared with species-rich Zanzibar, which is
24 likely explained by a combination of regional, historical, and habitat factors. Within each island
25 region, the diversity and composition of benthic assemblages vary along a habitat topographic
26 gradient, with a primary distinction between reefal and non-reefal habitats. Furthermore, across
27 two regions with almost completely different faunas, the ecological composition of ostracod
28 assemblages seems to follow strong and consistent controls of benthic community in terms of
29 the relative cover of coral, algae, and bare sand bottoms. The STP ostracod fauna shows high
30 level of endemism within and beyond tropical east Atlantic, indicating the mid-Atlantic Barrier
31 and Benguela Current as effective biogeographic filters. Thus, our trans-regional investigation
32 of the exotic oceanic islands contributes to important knowledge about the general patterns and
33 determinants of such isolated, peripheral marine ecosystems.

34

35 **1 Introduction**

36 Near-shore oceanic islands are of particular ecological and conservation importance for their
37 unique roles as dispersal nodes and reservoirs of marine benthic diversity (Cowie and Holland,
38 2006). The São Tomé–Príncipe Archipelago (STP) in the tropical East Atlantic (TEA) and the
39 Zanzibar Archipelago in the western Indian Ocean (WIO) represent two such systems situated
40 in western and eastern sides of equatorial Africa, respectively. They are in highly comparable
41 geographic settings (i.e., close to the African continent at equatorial latitudes) and broadly
42 similar environmental conditions (i.e., tropical shallow marine) (Da Costa et al., 2022; Tian et
43 al., 2024a), which make them natural analogues for contrastive studies of marine diversity and
44 community structure (Table 1 and Fig. 1). These archipelagos provide important offshore



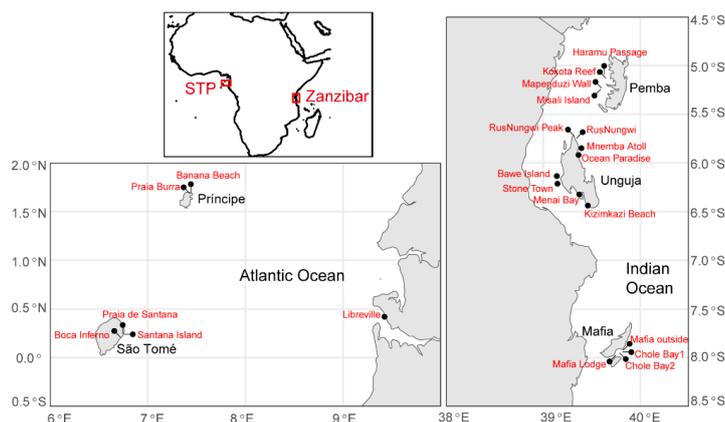
45 habitats and nursery areas for coastal and pelagic organisms (Da Costa et al., 2022). Isolated
 46 but not distant from the continent, they may support certain levels of endemism while
 47 maintaining connectivity with surrounding shelf ecosystems (Maia et al., 2018). As recipients
 48 and redistributors of tropical biotas via equatorial currents, these islands function as
 49 steppingstones to promote faunal exchange across biogeographic provinces (Cowie and
 50 Holland, 2006; Fajemila and Langer, 2017). At the same time, both the STP and Zanzibar
 51 ecosystems provide essential marine resources to local communities but face severe over-
 52 exploitation and habitat degradation, in conjunction with anthropogenic climate changes (Da
 53 Costa et al., 2022; Bravo et al., 2021).

54

55 Table 1. Comparison of the STP and Zanzibar archipelagoes. Temperature and salinity (annual
 56 mean of surface value) from the World Ocean Atlas 2023 (Reagan et al., 2024) and net primary
 57 productivity from the Ocean Productivity Website
 58 <https://orca.science.oregonstate.edu/index.php>. Shoreline data used to calculate all geographic
 59 parameters from <https://www.naturalearthdata.com>.

	Region	Temperature °C	Salinity	Net primary productivity (mgC/m ² /day)	Coastline length (km)	Land area (km ²)	Distance to continent (km)
STP	West Africa	26.27	33.95	1576	185	1042	243
Zanzibar	East Africa	27.32	35.11	504	767	3002	49

60



61

62 Fig. 1. Map showing the STP Archipelago in western Africa and the Zanzibar Archipelago in
 63 eastern Africa with ostracod sampling locations.

64

65 At a larger spatial scale of biogeographic province, the biotic and abiotic contexts of these two
 66 archipelagoes diverge sharply. The TEA is one of the least studied marine tropical provinces
 67 characterized by low biodiversity, high productivity, and pronounced endemism (Da Costa et
 68 al., 2022; Floeter et al., 2008; Polidoro et al., 2017). Environmentally, it is featured by complex
 69 hydroclimatic conditions. Cold boundary currents (Canary in the north and Benguela in the
 70 south) and seasonal upwelling along western African coast restrict the geographic range of true
 71 tropical regions (Da Costa et al., 2022; Polidoro et al., 2017). Biogeographically, the TEA has



72 a long history of isolation with the opening of the Atlantic separating it from South America
73 since early Jurassic; the closure of the Tethyan Seaway disconnecting it with Indo-Pacific realm
74 during the Miocene; and finally, the establishment of the Benguela Current isolating it from
75 southern Indian Ocean during the Pliocene (Floeter et al., 2008; Cowman et al., 2017). On the
76 eastern side of tropical Africa, however, the western Indian Ocean (WIO) harbors a much richer
77 shallow-marine fauna typical of coral reefs and reef-associated environments under the
78 influence of warm Agulhas Current (Obura, 2012). The tropical section of the WIO exhibits a
79 moderate level of endemism in the periphery of vast Indo-Pacific realm, with biogeographic
80 affinity to both the Red Sea and central Indo-Pacific (Obura, 2012; Cowman et al., 2017). It is
81 expected that the differences between the TEA and WIO at large regional scale should lead to
82 idiosyncratic patterns in the diversity and composition of the STP versus Zanzibar faunas.

83

84 Despite their importance, a huge gap lies in our understanding of these remote oceanic islands.
85 The studies of STP marine biodiversity have focused primarily on conspicuous groups of high
86 economic and cultural values, such as fishes, turtles, and cetaceans (Da Costa et al., 2022;
87 Carvalho et al., 2022; Ferreira-Airaud et al., 2022). Coastal and nearshore-pelagic fishes have
88 been examined from ecological aspects for their diversity distribution and faunal composition
89 (Porriños et al., 2024; Otero-Ferrer et al., 2020; Maia et al., 2018; Canterle et al., 2020; Tuya
90 et al., 2017), but most other taxa are only known from fragmentary checklists. The Zanzibar is
91 comparatively better studied for its diverse and productive reef ecosystems, with sporadic
92 island-scale monitoring of reef ecological health (Bravo et al., 2021; Larsen et al., 2023;
93 Grimsditch et al., 2009). Apart from corals and reef fishes, however, the majority of benthic
94 diversity remains undocumented across habitats and environmental gradients. Therefore, an
95 integrated and systematic investigation with multiple model organisms is urgent necessity for
96 both island regions to advance our understanding of these novel biological systems and their
97 controlling factors. It is also an important step towards effective conservation management of
98 these island ecosystems for their ecological and economic value.

99

100 In addition to conspicuous macroinvertebrates and fish, benthic meiofaunal groups such as
101 Ostracoda and foraminifera have been increasingly used as model proxies in macroecological
102 studies. They are of high ecological importance, taking up a large proportion of total marine
103 biodiversity (Leray and Knowlton, 2015) and performing critical ecosystem functions (Prazeres
104 and Renema, 2019). Despite one being metazoan (ostracod) and the other protist (foraminifera),
105 they show consistent diversity and biogeographic patterns across spatial-temporal scales and
106 serve as surrogates for benthic fauna as a whole (Yasuhara et al., 2017; Mamo et al., 2023; Tian
107 et al., 2024b; Baldrighi and Manini, 2015). They respond reliably and sensitively to
108 environmental gradients and thus have high utility as bioindicators (Mamo et al., 2023; Hong
109 et al., 2022). Last but not least, these meiofaunas leave extremely rich fossil records, which
110 make them the ideal proxy to reconstruct historical changes and assess human impacts on
111 biosphere over decades to hundreds of years (Yasuhara et al., 2017). In this study, we present
112 the first island-scale survey of ostracods from STP and integrate these results with published
113 ostracod data from Zanzibar and foraminifera data from both archipelagos. We compared alpha,
114 beta, and gamma diversity patterns across regions and taxa to probe into the ecological and
115 environmental structuring of benthic communities. We investigated habitat and physical
116 controls of faunal compositions in reefal versus non-reefal ecosystems. Finally, we discussed
117 the biogeographic affinity of STP within the TEA and with other tropical Atlantic provinces.
118 Together, this study contributes to valuable knowledge on exotic island biotas and explores
119 universality versus specificity in their biological patterns and drivers.



120

121 **2 Material and methods**

122 2.1 Regional setting

123 The São Tomé-Príncipe Archipelago is located along the Cameroon Volcanic Line at 243 km
124 off the continental West African coast in the Gulf of Guinea (Canterle et al., 2020) (Fig. 1; Table
125 1). It consists of two main islands, São Tomé and Príncipe, with a coastline extension of 185
126 km and total land area of 1042 km². Biogeographically, the archipelago is part of the Guinea
127 Current Large Marine Ecosystem extending from Guinea Bissau to Angola within the Tropical
128 East Atlantic (TEA) province (Fajemila and Langer, 2017). It is influenced by three incoming
129 currents, namely the Gulf of Guinea Current from North, the Benguela Current from South, and
130 the easterly flowing Equatorial Counter Current (Da Costa et al., 2022). The convergence of
131 ocean currents causes seasonal equatorial upwelling and dominates regional productivity
132 (Friedlander et al., 2014). Freshwater and particulate discharge from main rivers (Ogooué and
133 Congo) leads to great spatial-temporal variations in salinity and turbidity in coastal waters
134 (Friedlander et al., 2014). Steep environmental gradients occur across the upper water column,
135 with temperature reaching typical tropical ranges of 25-29 °C at surface while dropping to ~20 °C
136 below a constant thermocline at depths of 20-30 m, and likewise for salinity and nutrient content
137 among other parameters (Maia et al., 2018). As constrained by regional hydrological conditions,
138 no extensive matrix of true coral reefs exists in the Gulf of Guinea including STP, instead the
139 benthic habitats are characterized by a mosaic of scattered rocky reefs colonized by various
140 hard corals, turf algae, macroalgae, and sponges (Otero-Ferrer et al., 2020). Mangroves and
141 seagrass beds are the other two major habitats along the islands' coast. In terms of substratum,
142 a large proportion of the coastal area is covered by dark-colored volcanic sands in contrast to
143 stable quartz sands and calcareous bioclastic sands.

144

145 The Zanzibar Archipelago is situated 49 km away from the Tanzania mainland along the East
146 African coast (Narayan et al., 2022) (Fig. 1; Table 1). The three main islands, Pemba, Unguja,
147 and Mafia measure a total land area of 3002 km² and a coastline of 767 km. The archipelago
148 belongs to the Somali Coastal Current Large Marine Ecosystem that stretches from Somalia to
149 the northeastern coast of South Africa in the western Indian Ocean (WIO) province (Thissen
150 and Langer, 2017). Major currents influencing this region include the westward-flowing South
151 Equatorial Current and the northward-flowing East African Coastal Current (Tian et al., 2024a).
152 The tropical monsoonal climate regulates annual temperature variation between 25-29 °C with
153 humid and dry seasons (Narayan et al., 2022). The Zanzibar islands possess one of the largest
154 reef areas along the coast of East Africa, but many local reefs are in early-middle stages of
155 degradation because of increasing marine pollution and urbanization, especially in heavily
156 populated Stone Town areas (Grimsditch et al., 2009; Bravo et al., 2021; Larsen et al., 2023).
157 Shallow fringing reefs and deep fore reefs are the most common habitat, followed by vegetated
158 sand flats and mangroves. The substratum is primarily calcareous bioclastic sands in fine to
159 medium grain size with varying amounts of reef rubble, or otherwise fine quartz sands.

160

161 2.2 Sample processing and data integration

162 In total ten surface sediment samples were collected from the Sao Tome and Principe islands in
163 addition to one sample along continental coast in Libreville directly east of the archipelago (Fig.
164 1). These samples cover a depth range of 0.5-30 m across the tidal and subtidal zones and
165 represent the habitat types of marginal fringing reefs, sand flats, and mangroves. Samples were



166 collected by scuba diving to scrape along the seabed and fill plastic containers with top 2 cm of
 167 the surface sediments, in order to avoid the loss of finer particles due to suspension. In the
 168 laboratory, sediments were washed through a 63 μm sieve, oven dried at 50 $^{\circ}\text{C}$, and dry sieved
 169 over a 150 μm mesh sieve. Subfossil ostracods were picked from the > 150 μm size fraction
 170 and a single valve or a carapace was treated as one individual, which is the standard method in
 171 ostracod research (Tian et al., 2024a). Specimens preserved with soft parts (live) were counted
 172 together with the empty ones (dead) to make up the total, time-averaged assemblage, which is
 173 proven to effectively define benthic habitats (Tian et al., 2024a). In the next step, we integrated
 174 the census count of STP ostracods with previously published ostracod data from Zanzibar after
 175 rigorous taxonomic standardization (Tian et al., 2024a). Published foraminifera data from the
 176 two regions were integrated in the same way so that we build a trans-regional, multi-proxy,
 177 large-size dataset of benthic meiofaunas (Thissen and Langer, 2017; Fajemila and Langer,
 178 2017).

179

180 To evaluate the biogeography of STP and more generally the TEA, we compiled species
 181 occurrence data of the Recent and sub-Recent shallow-marine ostracods for five tropical-
 182 subtropical provinces in the Atlantic Ocean through extensive literature search (Table 2). The
 183 geographic delineation of each province follows Floeter et al. (2008) and Le Lœuff and Von
 184 Cosel (1998). Ostracod fauna of each province was compared for common species as indication
 185 of biogeographic link. The authors are fully aware that the compiled species list is not
 186 exhaustive and in fact many areas are poorly studied for ostracods, which leads to unavoidable
 187 sampling bias. Nevertheless, it is believed that such compilation gives an overview of the
 188 biogeographic relationship among provinces and hints at the evolutionary process underlying.

189

190 Table 2. Definitions of tropical-subtropical biogeographic provinces of the Atlantic Ocean (Le
 191 Lœuff and Von Cosel, 1998; Floeter et al., 2008) and shared number of species with STP. See
 192 Table S4 and supplementary data for the complete species occurrence list and literature cited.

Province	Geographic range	Climate	No. species	No. common species with the STP
Northwestern Atlantic	Caribbean, North American coast to Carolina	Tropical-subtropical	470	7
Southwestern Atlantic	Brazil and Brazilian oceanic islands	Tropical-subtropical	195	8
Northeastern Atlantic	Western African coast from Gibraltar to Cape Blanco, Mediterranean	Subtropical	497	7
Tropical East Atlantic	Western African coast from Cape Blanco to Moçâmedes, Gulf of Guinea	Tropical	151	22
Southeastern Atlantic	Western African coast from Moçâmedes to Cape of Good Hope	Subtropical	266	3

193

194 2.3 Quantitative analyses

195 For ostracod diversity measures, we used Hill numbers (i.e., the effective number of equally
 196 abundant species) parameterized by a diversity order q (Chao et al., 2014a). The order q
 197 determines how much weight is given to the relative abundance of species. Specifically, the



198 Hill number (0D) reduces to species richness for $q=0$; the Hill number (1D) measures the
199 diversity of the abundant species for $q=1$; and the Hill number (2D) measures the diversity of
200 dominant species for $q=2$ (Chao et al., 2014a). To tackle the problem of unequal sample efforts
201 among ostracod assemblages and datasets, we standardized the Hill numbers with rarefaction
202 or extrapolation to the largest sample completeness possible for alpha diversity across samples
203 (82.5 %) and gamma diversity across regions (96.7 %) (Chao et al., 2014b). Multiplicative beta
204 diversity was calculated as gamma diversity divided by alpha per sample, which quantifies the
205 extent of among-assemblage differentiation in faunal composition (Chao et al., 2023). The
206 mean and 95% confidence intervals of the Hill numbers were estimated by bootstrap resampling
207 with 100 repetitions. Species evenness was computed based on the slope of the Hill number
208 profiles as a function of order q (Chao and Ricotta, 2019). In an even assemblage, the species
209 richness and number of abundant and dominant species are similar, resulting in a more gradual
210 slope. In contrast, an uneven assemblage is dominated by one or a few species, leading to a
211 steeper slope. The species evenness or the normalized slopes of Hill number profiles were
212 computed at orders $q=1$ (1E) and $q=2$ (2E).

213

214 We used the Generalized Additive Mixed-effect Model (GAMM) to investigate effective
215 environmental controls of ostracod alpha diversity in each region. The environmental variables
216 used in GAMM include habitat topographic type, algae coverage, and sediment type as habitat
217 factors, along with human impact, water depth, and distance to land as physical factors. Each
218 of these factors has been shown to influence the diversity distribution of benthic organisms
219 (Porriños et al., 2024; Otero-Ferrer et al., 2020). All variables were measured on site except for
220 distance to land, which was computed based on the distance between sampling coordinates and
221 shoreline data from <https://www.naturalearthdata.com>. The GAMM used penalized cubic
222 regression spline smooths with restricted maximum likelihood (REML) method (Wood, 2024).
223 In addition to water depth and distance to land as numeric variables, habitat type (fore reef,
224 fringing reef, back reef, sand flat, and mangrove) and sediment type (bioclastic sand, fine-
225 grained sand, and volcanic sand) were treated as categorical variables. Algae coverage and
226 human impact were handled as ordinal variables with three levels (i.e., low, medium, and high).
227 GAMM estimated the fixed effects of these environmental factors on the diversity patterns. It
228 also incorporated a random factor of island by smooths, as penalized regression terms. The
229 evaluation of random effects helped to distinguish whether differences in biodiversity are due
230 to site-specific conditions or are more uniformly affected by fixed factors (Wood, 2024). The
231 comparison and ranking of GAMM models were based on AICc, which is an adjustment of the
232 standard Akaike Information Criterion (AIC) incorporating a correction for small sample sizes.
233 Relative model support was measured by the Akaike Weights (weight) (Anderson et al., 2000),
234 with a higher value denoting a better fit to the data for a given number of model parameters.
235 The parameter estimates were averaged across all candidate models weighted by their relative
236 support. This approach accounted for uncertainty in model selection and provided appropriate
237 confidence intervals (Anderson et al., 2000). The relative importance of a predictor variable
238 was then determined by summing the Akaike weights of all the models in the candidate set in
239 which that specific predictor variable occurred. The summarized top model was validated for
240 normality and homogeneity. The spatial autocorrelation in model residues was examined by
241 Moran's I statistic with a permutation test. No significant spatial autocorrelation was detected
242 in the top model.

243

244 To evaluate faunal variation among ostracod assemblages, we conducted hierarchical cluster
245 analysis based on Ward's minimum variance and Hill-number-based dissimilarity indices (1-



246 C_{qN}), where N indicates the number of assemblages for comparison and order q determines the
247 indices' weight on relative abundance (Chao et al., 2014a). Depending on the parameter q , the
248 Sørensen ($q=0$), Horn ($q=1$), and Morisita–Horn ($q=2$) indices measure compositional
249 dissimilarity in terms of species presence-absence, abundant species, and dominant species,
250 respectively (Chao et al., 2014a). The optimal number of clusters was determined at which the
251 average silhouette width is highest, indicating cohesion within a cluster and separation between
252 clusters. We identified the top 10 indicator species of each cluster based on the Indicator Value
253 (IndVal), as defined by (Dufrêne and Legendre, 1997; Cáceres and Legendre, 2009).
254 Specifically, the IndVal was calculated as the square root of the product of relative abundance
255 (i.e., specificity) and relative frequency (i.e., fidelity) of a species present in the defined group.
256 The faunal composition of each sample was illustrated with a heat map showing the abundance
257 (species count after applying a fourth root transformation) of the top 10 indicator species of
258 each cluster, with the relationship between species determined by Hellinger distances. To
259 examine faunal compositional changes across environmental gradients in each region, we
260 performed non-metric multidimensional scaling (nMDS) based on the Sørensen, Horn, and
261 Morisita–Horn dissimilarity indices and calculated the correlations between environmental
262 variables and MDS axes with permutation tests. We also used Distance-based Redundancy
263 Analysis (dbRDA) to measure the variance explained by each environmental variable and thus
264 identify significant determinants of faunal structure.

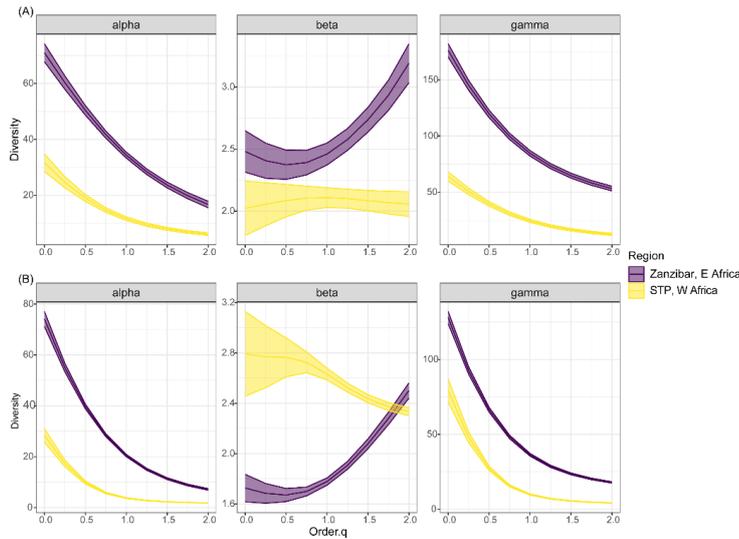
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266 All statistical analyses were replicated on the foraminifera data in exactly the same manner.
267 Samples of low abundance (<50 individuals) were excluded from all quantitative analyses. All
268 analyses were implemented in R (R Core Team, 2025) and RStudio (Rstudio, 2016) using
269 *tidyverse*, *iNEXT*, *mgcv*, *MuMIn*, *hillR*, *indicspecies*, *pheatmap*, and *vegan* packages.

270

271 **3 Results**

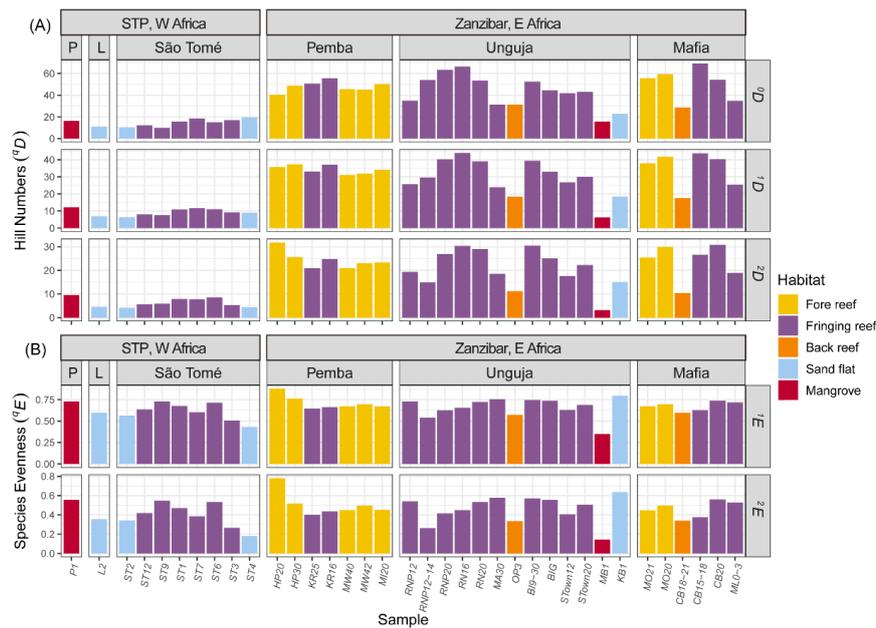
272 Eleven samples from the STP Archipelago region yielded 2596 ostracods of 90 species. After
273 integrating published ostracod data from Zanzibar, the resultant trans-regional dataset has 8858
274 ostracods under 306 species. The integrated foraminifera dataset of these two regions is of a
275 larger sample size (22515 individuals) but a lower species number (251). First of all, the most
276 striking pattern is the depauperation of STP fauna compared with exceedingly diverse Zanzibar
277 fauna. For both taxonomic groups, Zanzibar alpha diversity is more than twice the STP value
278 at each order q (Figs. 2-4). At the regional level, Zanzibar gamma diversity is also markedly
279 higher than that of STP, but this regional difference is more pronounced as recorded by
280 ostracods than by foraminifera, especially at order $q=0$ (Fig. 2). Beta diversity shows more
281 complicated and contrasting patterns based on two organisms, however. In the case of ostracods
282 at orders $q=0$ and $q=1$, Zanzibar has a slightly yet significantly higher beta diversity than STP
283 (i.e., non-overlapping 95% confidence intervals); only towards order $q=2$ that the regional
284 difference is conspicuous, indicating a higher variability of ostracod assemblages in terms of
285 dominant species in Zanzibar. Interestingly, for foraminifera, beta diversity profiles of the two
286 regions display opposite trends across the orders q (STP declining while Zanzibar increasing)
287 so that the STP has higher diversity at orders $q=0$ and $q=1$ but not $q=2$. Indeed, in STP, high
288 variability of rare species among foraminifera assemblages contributes to a comparatively large
289 regional species pool (gamma) without an increase in local (alpha) diversity.



290

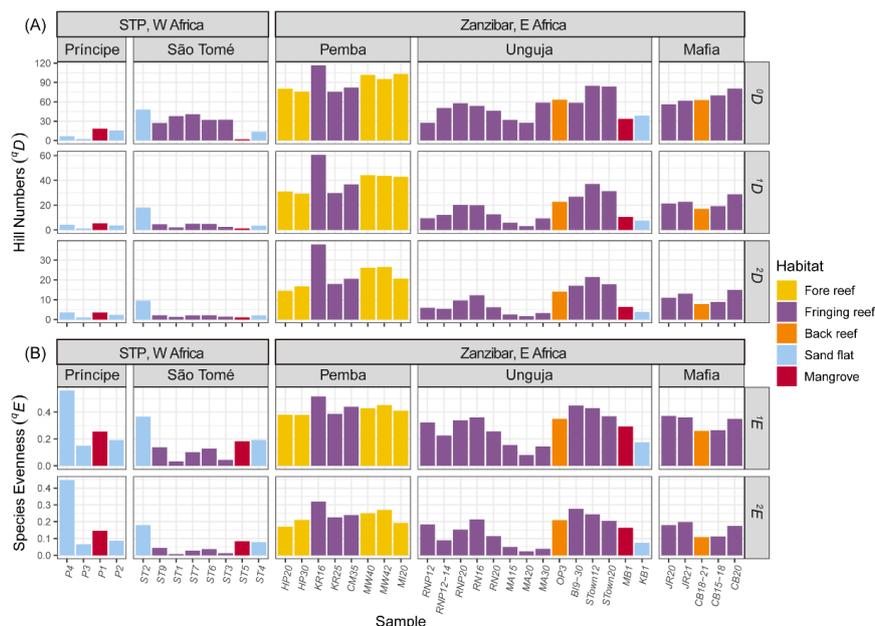
291 Fig. 2. Alpha, beta, and gamma diversity of the STP and Zanzibar regions for ostracods (A) and
 292 foraminifera (B) shown by Hill number profiles. Standardized sample coverage: ostracod 82.5%
 293 for alpha and beta, 96.7% for gamma; foraminifera 97.3% for alpha and beta, 98.9% for gamma.
 294 The shaded area shows the 95% confidence interval of the profile.

295



296

297 Fig. 3. Species diversity (A) and evenness (B) of ostracod assemblages across orders q from
 298 STP and Zanzibar. The two regions show significant differences in their diversity ($p < 0.001$) but
 299 not evenness ($p > 0.1$) across all orders. p-value given by ANOVA test. P: Príncipe; L: Libreville.



300

301 Fig. 4. Species diversity (A) and evenness (B) of foraminifera assemblages across orders q from
 302 STP and Zanzibar. The two regions show significant differences in their diversity ($p < 0.001$)
 303 and evenness ($p < 0.05$) across all orders. p -value given by ANOVA test.

304

305 Within each region, both groups show generally consistent patterns in their alpha diversity and
 306 species evenness across orders q , yet nuanced differences are also observed (Figs. 3-4). In STP,
 307 the diversity distribution of ostracods seems to be highly homogenous among different habitat
 308 types (Fig. 3A). Foraminifera diversity is generally high on fringing reefs, with one exception
 309 that the sand flat at ST2 is particularly diverse (Fig. 4A). In the much richer Zanzibar region,
 310 habitat control of species diversity is apparent for ostracods, as the highest diversity is found in
 311 some fringing reefs followed by fore reefs, while marginal back reefs, sand flat, and mangrove
 312 are much less diverse (Fig. 3A). Island difference in diversity is more conspicuous for
 313 foraminifera, however. All the fore and fringing reefs in Pemba consistently record a high
 314 number of species; in the other two islands, diversity on fringing reefs shows substantial
 315 variation, as some sites are moderately diverse while others (e.g., MA and RNP) have diversity
 316 as low as sand flat and mangrove (Fig. 4A). With regard to species evenness, diverse and
 317 depauperated ostracod assemblages are of equally high levels without an obvious region or
 318 habitat influence (Fig. 3B), suggesting similar faunal structure in terms of the proportion of rare
 319 and dominant species. Foraminifera display a more obscure pattern in their evenness, with large
 320 variations observed among individual samples. In particular, some fringing reefs (e.g., STs in
 321 the STP and MAs in Zanzibar) hold highly uneven foraminifera assemblages compared to all
 322 the rest reefal and non-reefal habitats (Fig. 4B).

323

324 Since the alpha diversity patterns of two groups in two regions show remarkable consistency
 325 across all orders q , in all statistical analyses below, we focus on the order $q=1$ for the diversity
 326 and corresponding dissimilarity measure, as it balances the richness and evenness components



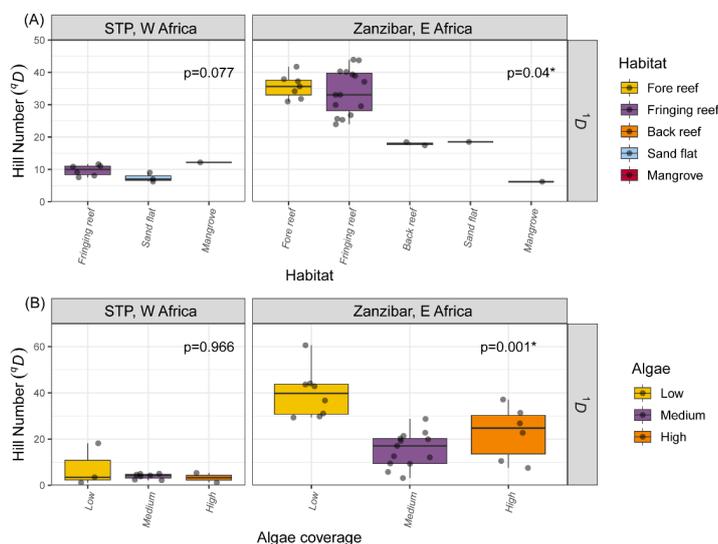
327 of diversity and thus has high ecological interpretability. All analyses for orders $q=0$ and $q=2$
 328 give generally consistent results and are put in the online supplementary materials for
 329 comparison (Tables S1-S2; Figs. S1-S6). First, results from GAMM modelling statistically
 330 support our raw observations (Figs. 3-4) and further reveal environmental controls of the alpha
 331 diversity patterns in two regions for two organisms. Habitat type is confirmed as the only
 332 significant determinant of ostracod diversity in Zanzibar, with the reefal habitats hosting more
 333 species than marginal and non-reefal ones (Table 3; Fig. 5A). Foraminifera instead show
 334 significant variations across the algae coverage gradient and across islands (Table 3; Fig. 5B).
 335 In particular, the algae effect is non-linear that diversity is lowest at medium coverage compared
 336 to low or high coverage. In STP, GAMM identifies no significant controls for both groups,
 337 which fits our expectations as their diversity distributions are largely homogenous along all
 338 environmental dimensions.

339

340 Table 3. Environmental controls of ostracod and foraminifera alpha diversity ($q=1$) in Zanzibar.
 341 Statistics from GAMM modelling showing the significant parameters in the averaged top model.
 342 RI: relative importance; L: linear term; Q: quadratic term.

Organism	Term	Estimate	Std. Error	t value	Pr(> t)	RI
Ostracod	(Intercept)	3.57	0.06	56.31	0	
	Habitat-Fringing reef	-0.05	0.08	-0.59	0.56	0.94
	Habitat-Back reef	-0.69	0.24	-2.81	0.01**	0.94
	Habitat-Sand flat	-0.66	0.33	-1.99	0.06	0.94
	Habitat-Mangrove	-1.75	0.97	-1.81	0.08	0.94
Foraminifera	(Intercept)	3.37	0.25	13.38	0	
	Algae coverage. L	-0.02	0.39	-0.06	0.95	0.83
	Algae coverage. Q	0.72	0.25	2.85	0.01*	0.83
	s(Island)	0.83	2	2.37	0.03*	0.85

343



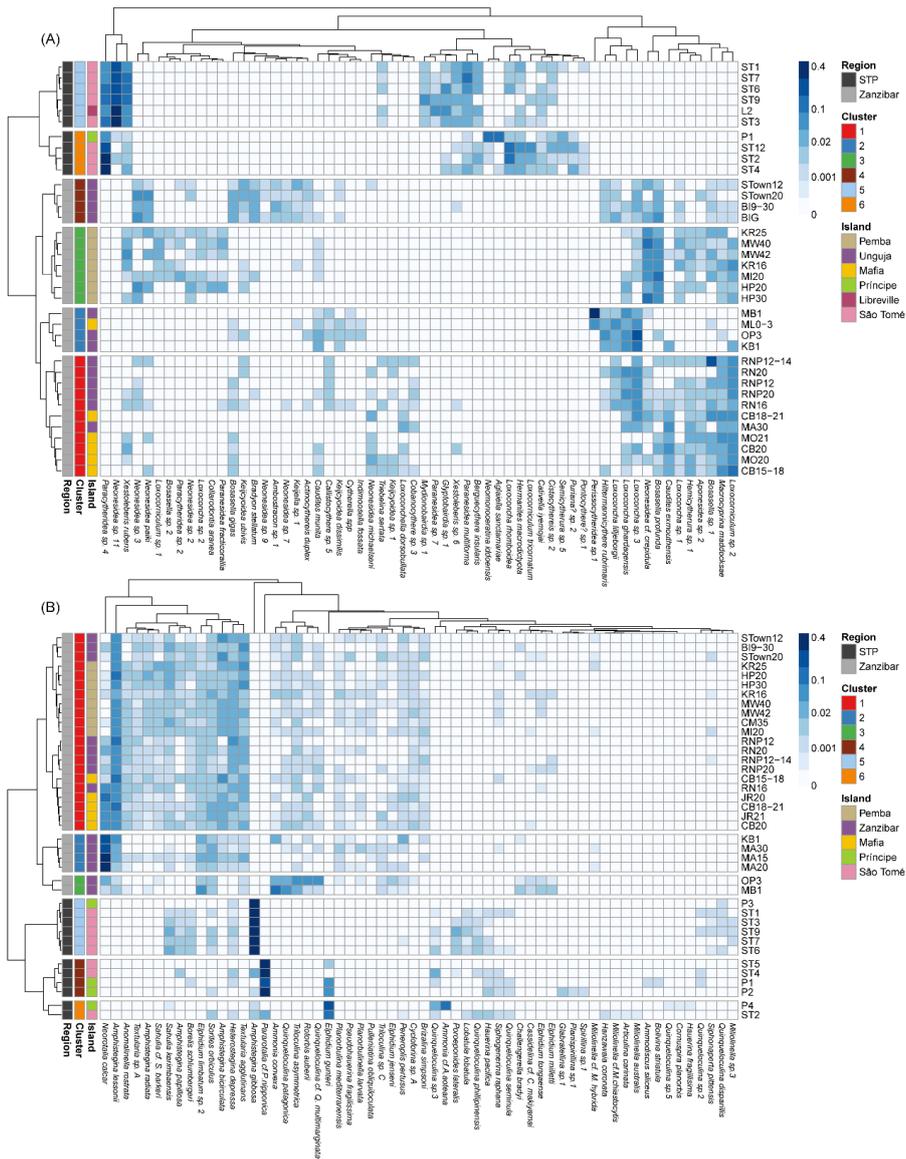
344

345 Fig. 5. Box plots showing variations in ostracod alpha diversity between habitat types (A) and
 346 foraminifera alpha diversity between algae coverage levels (B) for order $q=1$ in STP and
 347 Zanzibar regions. p-value given by the Kruskal-Wallis test.



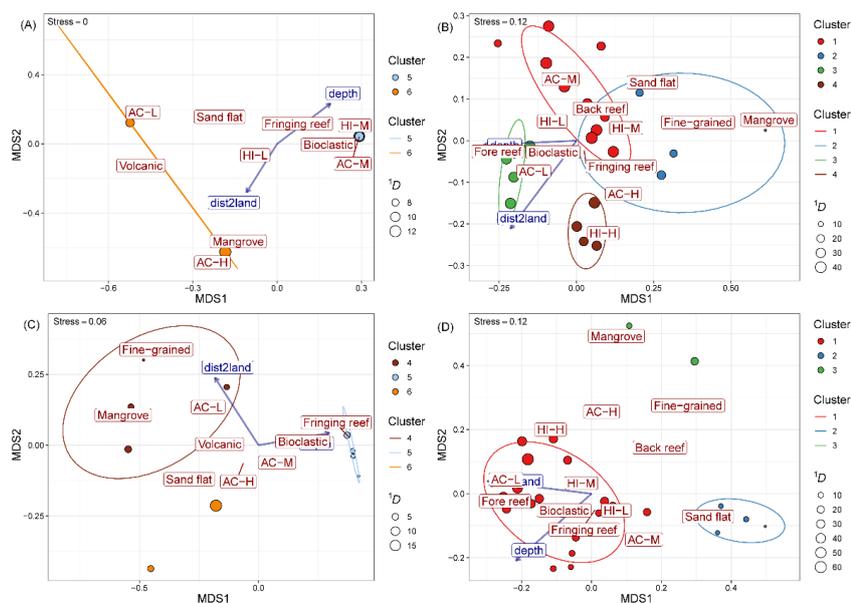
348

349 Next, the cluster analysis delineates six distinct clusters for both groups in two regions, and the
350 nMDS visualizes the separation of clusters correlated with environmental variables (Figs. 6-7).
351 In the case of ostracods, the Zanzibar and STP faunas are almost completely different with only
352 few species in common across regions (Fig. 6A). The ostracod assemblages in Zanzibar fall
353 into four clusters: C1 characterizes the fringing reefs of intermediate water depths, medium
354 algae cover, and medium human impact from Unguja and Mafia islands; C2 includes all shallow
355 samples from mangrove and sand flat habitats with high algae cover; C3 aggregates all the deep,
356 pristine fore reefs from Pemba Island with low algae cover and large distance off shore; and
357 lastly C4 is geographically confined to the Stone Town area near the center of human impact
358 (Figs. 6A and 7B). In STP, the two ostracod clusters clearly distinguish deep reefal (C5) and
359 shallow non-reefal assemblages (C6) (Figs. 6A and 7A). They also reflect variations in other
360 environmental dimensions such that C5 is bioclastic sand with medium levels of algae cover
361 and human impact while C6 is unique volcanic sand. The dbRDA analysis for ostracods in each
362 region consistently indicates that habitat type is the most important controlling factor of species
363 composition, followed by algae coverage and human impact (Table 4), whereas all other
364 parameters do not have a significant effect. In the case of foraminifera, there seems to be some
365 degree of faunal similarity between regions (Fig. 6B). The Zanzibar assemblages are separated
366 into three clusters: C1 clumps together all the true reefs in intermediate and deep waters across
367 all algae cover and human impact levels; C2 groups unique fringing reefs in Mnemba Atoll with
368 a sand flat; and C3 characterizes mangrove habitat with high algae cover (Figs. 6B and 7D).
369 Among three clusters in STP, C5 is typical of deep fringing reefs while C4 and C6 represent a
370 mixture of sand flat and mangrove habitats with all different levels of algae cover and various
371 sediment types (Figs. 6B and 7C). The dbRDA analysis for foraminifera reveals that habitat
372 type alone explains a large proportion of variances in faunal compositions in both regions,
373 although the effects of algae coverage, human impact, and distance to shore are also significant
374 in Zanzibar (Table 4).



375

376 Fig. 6. Composition of ostracod (A) and foraminifera (B) assemblages in STP and Zanzibar in
 377 terms of the top 10 indicator species of each cluster at order $q=1$. The blue heatmaps illustrate
 378 species count in each sample after applying a fourth root transformation. Dendrograms based
 379 on Horn dissimilarity between samples and Hellinger distances between species.



380

381 Fig. 7. nMDS ordination showing faunal variation correlated with environmental factors in each
 382 region for each organism. (A) STP ostracods; (B) Zanzibar ostracods; (C) STP foraminifera;
 383 (D) Zanzibar foraminifera. The vectors indicate correlations with continuous environmental
 384 variables and labels indicate the centroids of categorical environmental variables. AC: algae
 385 coverage; HI: human impact; H: high; M: medium; L: low. Color of each cluster as in Fig. 6.
 386 Size of sample dots represents alpha diversity at order $q=1$.

387

388 Table 4. Environmental controls of ostracod and foraminifera faunal composition ($q=1$) in
 389 Zanzibar and STP by dbRDA analysis. Only significant effects are shown.

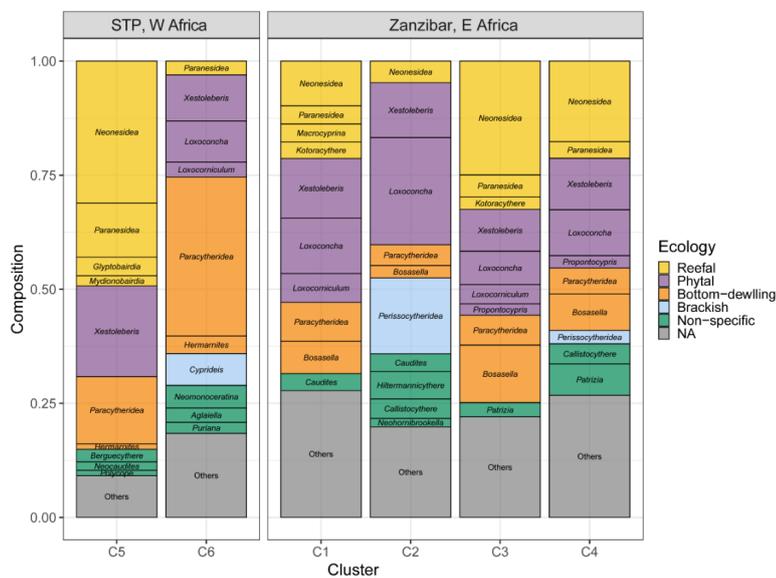
Organism	Region	Predictor	SumOfSqs	F value	Pr(>F)
Ostracod	Zanzibar, E Africa	Habitat type	1.36	5.11	0.001***
		Algae coverage	0.88	6.6	0.001***
		Human impact	0.57	4.28	0.001***
	STP, W Africa	Habitat type	0.46	17.06	0.009**
		Algae coverage	0.33	23.98	0.003**
		Human impact	0.22	16.49	0.002**
Foraminifera	Zanzibar, E Africa	Habitat type	0.81	8.97	0.001***
		Algae coverage	0.68	15.06	0.001***
		Human impact	0.45	10.01	0.001***
		dist2land	0.1	4.22	0.008**
	STP, W Africa	Habitat type	1.62	8.67	0.01**

390

391 Knowing that ostracod assemblages in both regions show primary distinction between reefal
 392 and non-reefal habitats, we examine the ecological composition of each cluster and compare
 393 between regions. We look into the top 10 genera of highest mean relative abundance in each
 394 cluster, since the ecology of individual species is often not understood, especially in STP where



395 a lot of new species are found, and also because genus-level patterns give more generality. The
 396 top 10 ostracod genera can be classified into five major ecological groups, which are coral reef
 397 affiliated, phytal, bottom dwelling, euryhaline, and the remaining non-specific (Fig. 8; Table
 398 S3). *Neonesidea* and family Bairdiidae in general typically inhabit coral reefs and reef-
 399 associated habitats in tropical shallow-marine environments (Titterton and Whatley, 1988;
 400 Whatley and Watson, 1988). These reefal genera are most abundant on the fringing reefs of C5
 401 in STP and the pristine fore reefs of C3 in Zanzibar, and secondarily on the fringing reefs of C1
 402 and C4 in Zanzibar. Phytal ostracods live on plant substrates including seagrass, macro algae,
 403 and turf algae (Kamiya, 1988). *Loxoconcha* and *Xestoleberis* as two well-known phytal genera
 404 (Keyser and Mohammed, 2021) dominate the mangrove and sand flat habitats of C2 in Zanzibar
 405 and weight similarly in their relative abundance among other clusters. On the contrary, sediment
 406 dwelling ostracods live on the surface of sand bottoms or the interstices of sand grains, with
 407 morphologically a flat ventral surface to adapt to their mode of life (Kamiya, 1988; Purper and
 408 De Orenellas, 1987). This group is represented by *Paracytheridea* in our samples, which is
 409 particularly abundant in the non-reefal habitats of C6 in STP. The euryhaline group consisting
 410 of *Perissocytheridea* and *Cyprideis* (Keyser, 1977; Wouters, 2017) is mostly confined to C2 in
 411 Zanzibar and C6 in STP, indicating possible brackish conditions of these shallow intertidal
 412 habitats. Thus, the reefal assemblages (C1, C3, C4, and C5) manifest great similarities in their
 413 ecological composition across regions, and likewise for non-reefal assemblages (C2 and C6),
 414 despite little taxonomic overlap of two regions.



415

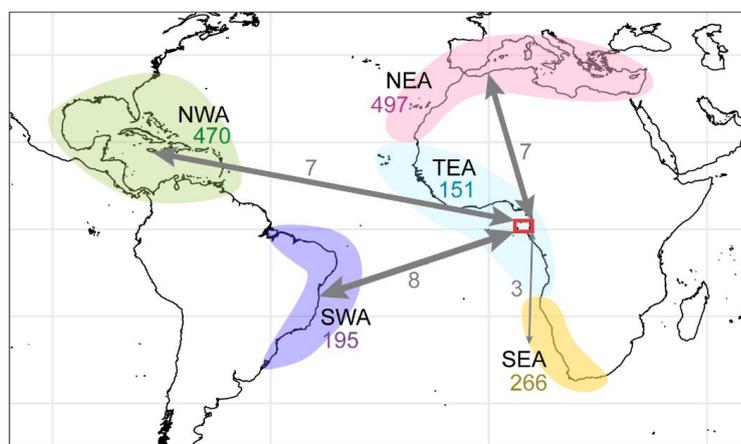
416 Fig. 8. Proportional composition of ostracod clusters at order $q=1$ with ecological groups shown
 417 by colors. The top 10 genera of highest mean relative abundance in each cluster are assigned to
 418 one of the ecological groups, i.e., reefal, phytal, bottom-dwelling, brackish, or non-specific. All
 419 genera other than the top 10 are grouped as 'Others' and their ecology is not considered. See
 420 Table S3 for genus autoecology and literature cited.

421

422 Our biogeographic investigation indicates that the ostracod fauna in STP has potentially a high
 423 level of endemism within and beyond the TEA province (Table 2; Fig. 9; Table S4). There are
 424 22 species in STP shared with tropical continental areas of west Africa, the Gulf of Guinea in



425 particular. The biogeographic connections of STP with all other Atlantic provinces are much
426 weaker, i.e., 7 species in common with the Northwestern and Northeastern Atlantic, 8 species
427 with the Southwestern Atlantic, and only 3 species with the Southeastern Atlantic. The STP and
428 Zanzibar faunas in our dataset overlap with 11 ostracod species and 16 foraminifera species, on
429 the other hand.



430

431 Fig. 9. Schematic map showing the biogeographic relationship of STP with tropical-subtropical
432 Atlantic provinces. Each colored number indicates the number of species described in each
433 province. Thickness of the arrow with number over it indicates connectivity by the number of
434 common species. Red box indicates STP. NWA: Northwestern Atlantic; SWA: Southwestern
435 Atlantic; NEA: Northeastern Atlantic; TEA: Tropical East Atlantic; SEA: Southeastern Atlantic.

436

437 4 Discussion

438 4.1 Impoverishment of the STP fauna in the TEA province

439 First of all, ostracods and foraminifera concordantly show exceptionally high Zanzibar diversity
440 in contrast to low STP diversity at both local (alpha) and regional (gamma) scales. This mirrors
441 broader patterns of species richness in the WIO versus TEA based on other benthic groups
442 (Cowman et al., 2017; Tittensor et al., 2010), confirming the usefulness of meiofaunal proxies
443 in macroecological studies. The impoverishment of STP fauna is likely due to environmental
444 and historical constraints acting in conjunction. In the TEA along the west African coast, cold
445 boundary currents and seasonal coastal upwelling restrict the geographic range of true tropical
446 segments (Da Costa et al., 2022) and also inhibit the growth of large coral reefs where high
447 benthic diversity is usually located (Friedlander et al., 2014). Moreover, the coastline is mostly
448 straight, and the continental shelf is very narrow and dominated with monotonous sandy and
449 muddy bottoms (Polidoro et al., 2017; Friedlander et al., 2014). In fact, the TEA has the smallest
450 shelf area of the world's main tropical regions (Polidoro et al., 2017). Small habitat areas may
451 not support high biodiversity as predicted by the species-area relationship (Losos and Schluter,
452 2000), and low habitat complexity limits the potential of allopatric speciation (Bellwood et al.,
453 2012). Over the evolutionary history of the TEA, increasing isolation had made it difficult to
454 receive species from other regions, especially the biodiversity hotspots in Caribbean and
455 broadly Indo-Pacific realm (Floeter et al., 2008). All these environmental and biogeographic
456 factors disfavor the origin and preservation of high biodiversity, and together they may account



457 for the depauperation of the TEA province and subsequently the low diversity in STP, since the
458 oceanic islands are integral components of larger biogeographic regions.

459

460 In contrast to an explicit, unambiguous pattern of regional differences in alpha and gamma
461 diversity, beta diversity of STP and Zanzibar shows inconsistent variations across orders q for
462 ostracods and foraminifera, which implies some ecological distinction between two groups and
463 different mechanisms underlying their community assembly (Fig. 2). For ostracods, across the
464 regional diversity gradient, it appears that the richness of local assemblage approximately scales
465 to the size of regional species pool (i.e., similar levels of beta diversity at $q=0$ in two regions),
466 indicating that the ostracod communities are regionally enriched (Devantier et al., 2020). Strong
467 evidence for regional enrichment of biodiversity has been found in corals and marine epifaunal
468 invertebrates in general (Devantier et al., 2020; Witman et al., 2004), and it is widely
469 acknowledged that local diversity is shaped by processes operating on larger spatial scales. At
470 Order $q=2$, however, elevated beta diversity of dominant species in Zanzibar may reflect a
471 higher habitat diversity there, as the dominant species are usually well-adapted to certain
472 habitats. The transitions from mature to marginal reefs and eventually to non-reefs across a
473 large environmental gradient correspond to fundamental shifts in the well-adapted ostracod
474 composition. Unexpectedly for foraminifera across two regions, beta diversity is higher in STP
475 at orders $q=0$ and $q=1$ with a comparatively large regional species pool yet low local richness.
476 Instead of a saturation effect on local assemblages, i.e., biotic interactions limit the number of
477 species that may coexist locally (Devantier et al., 2020), it is more likely that certain
478 environmental filtering determines the spatial patterns of species occurrence as many species
479 have narrow and specific habitat ranges in STP (Fajemila and Langer, 2017). For example,
480 *Ammonia* cf. *A. aoteana* is exclusively found in the sand flat of P4 while *Glabratellina* sp.1
481 is specific to the sand flat of P2 (Fig. 6B). Strict environmental structuring of foraminifera
482 assemblages for rare and abundant species thus translates to profound changes in species
483 composition across sites, which collectively add up to a comparatively large regional species
484 pool in STP. The scenario in Zanzibar is quite the opposite that low beta diversity at orders $q=0$
485 and $q=1$ is accounted by homogenous species distributions among most of the reefal habitats.
486 Finally at order $q=2$, STP and Zanzibar foraminifera reach similar levels of beta diversity with
487 each cluster dominated by few well-adapted species (e.g., *Neorotalia calcar* in C2, *Pararotalia*
488 cf. *P. nipponica* in C4, and *Amphistegina gibbosa* in C5) (Fig. 6B) (Fajemila and Langer, 2017;
489 Thissen and Langer, 2017). Comparing the beta diversity patterns of two taxonomic groups,
490 our results tentatively indicate that the local-regional relation of biodiversity may be twisted by
491 environmental conditions for different organisms depending on their ecology.

492

493 4.2 Environmental control of local diversity and faunal composition

494 The GAMM modelling reveals that environmental effects on local diversity vary between two
495 organisms and between two regions (Table 3). In Zanzibar, ostracod local diversity is regulated
496 by habitat type as the fore and fringing reefs with high topographic complexity support more
497 diverse assemblages compared to marginal reefs, mangroves, and featureless soft bottom
498 habitats (Fig. 5A). Diversity is particularly high on some fringing reefs with medium algae
499 coverage (e.g., RNs and CBs) (Fig. 3A), likely because interlaced hard corals, macro algae, and
500 turf algae offer diverse and heterogenous microhabitats to accommodate different ecological
501 groups (Tian et al., 2024a). It is intriguing that the local diversity of foraminifera in Zanzibar
502 responds nonlinearly to the algae factor with the lowest diversity at medium coverage (e.g.,
503 MAs and RNPs) (Figs. 4A and 5B). In fact, many sites with medium algae coverage can be
504 characterized as transitional environments between hard and soft bottoms, where the sediments



505 are homogenous, medium-grained bioclastic sands. These sites are idiosyncratic in terms of not
506 only diversity but also composition (e.g., the MAs form its own foraminifera cluster C2) (Fig.
507 6B). Neither reefal nor phytal foraminifera flourish in such environments, so that local diversity
508 records the lowest level. This is in sharp contrast to the ostracod pattern that various ecological
509 groups overlap in algae-covered reefal habitats to achieve high diversity, which conforms to the
510 classic intermediate disturbance hypothesis (Viljur et al., 2022; Townsend et al., 1997). A
511 possible explanation for foraminifera being a contrarian in this regard is that they may have
512 high ecological specialization and specific habitat requirements, which make them avoid
513 transitional algae-covered environments. Then, in STP, the local diversity of both groups does
514 not evidently follow any environmental regulations tested (Fig. 5). Diversity distribution is
515 essentially uniform for ostracods while site-specific for foraminifera. As the seascape is
516 predominantly sandy and muddy bottoms along the west African coast (Friedlander et al., 2014),
517 small fringing reefs in STP may provide one of the few hard substrates in this region for reef
518 organisms yet they lack the topographic complexity required to host high diversity like true
519 tropical coral reef ecosystems. Consequently, there are no locally diverse benthic assemblages
520 in STP.

521

522 The dbRDA analysis demonstrates that environmental controls over faunal composition are
523 highly concordant for two organisms in two regions, with habitat type being of overwhelming
524 importance (Table 4). Reefal and non-reefal assemblages are fundamentally divergent as they
525 show widest separation in cluster and nMDS analysis (Figs. 6-7). Among various types of reefal
526 habitats, algae coverage further differentiates local assemblage compositions, as the pristine
527 Pemba reefs dominated by hard corals (ostracod cluster C3) have lower abundance of phytal
528 species as compared to all other moderately algae-covered reefs. The effects of human impact
529 are weaker and mostly apparent at the highest level of disturbance, as the Stone Town sites
530 (ostracod cluster C4) are characterized by some Trachyleberididae genera (e.g., *Actinocythereis*)
531 but their ecological significance is not well understood in this case (Tian et al., 2024a). Thus,
532 the delineation of ostracod clusters directly and specifically reflects the interacting effects of
533 habitat, algae, and human factors. With regard to foraminifera, apart from aforementioned
534 environmental drivers, distance to land also explains a minor proportion of faunal variance in
535 Zanzibar, as indicated by the dominance of opportunistic taxa (e.g., *Ammonia convexa*) in
536 nearshore lagoonal and mangrove sites (foraminifera cluster C3) (Thissen and Langer, 2017).

537

538 Despite distinct taxonomic compositions of the STP and Zanzibar faunas at species and even
539 genus level, there is a marked inter-regional convergence in the ecological structure of ostracod
540 reefal and non-reefal assemblages in terms of the proportions of coral, phytal, bottom-dwelling,
541 and euryhaline taxa (Fig. 8). The fringing reef cluster (C5) in STP and pristine fore reef cluster
542 (C3) in Zanzibar both show highest abundance of coral affiliated taxa, while the other two reefal
543 clusters with algae cover (C1 and C4) in Zanzibar have comparatively more phytal taxa besides
544 coral taxa. Regarding the non-reefal clusters, C6 in STP is dominated by bottom-dwelling and
545 secondarily phytal taxa, in addition to a small proportion of euryhaline and almost no coral taxa.
546 C2 in Zanzibar is instead comprised of primarily phytal taxa followed by euryhaline and lastly
547 bottom-dwelling taxa. The discrepancy between non-reefal clusters C6 and C2 is likely caused
548 by low vegetation coverage in the sand flat habitats in STP, where sea floor is mostly bare, so
549 that the bottom-dwelling taxa thrive while the phytal taxa perish. The exclusive occurrence of
550 euryhaline taxa in the non-reefal intertidal clusters indicates salinity variations there, in contrast
551 to normal marine conditions in deeper subtidal environments. Our trans-regional comparison
552 clearly demonstrates a persistent correspondence between ostracod ecological structure and



553 environmental character. Specifically, the relative abundances of coral-affiliated, phytal, and
554 bottom-dwelling taxa seem to vary predictably along a benthic community gradient depending
555 on the percentage coverage of hard corals, algae and bare sands. Although more studies from
556 other regions are imperative to test the generality of this pattern, the findings presented here are
557 considered illuminating. Ostracods can potentially be an indicator of reef condition to track the
558 degradation from coral- to algae-dominated states (Tian et al., 2024a), if a quantitative
559 correlation is established between ostracod ecological composition and benthic community in
560 tropical reefs and reef-associated habitats.

561

562 4.3 Biogeography of STP ostracods

563 Our data suggests high endemism of STP ostracods since many new species (52 out of 90) are
564 found here. However, undersampling of the TEA ostracods complicates firm conclusions and
565 chances are that some of our species may actually have undocumented distributions in coastal
566 West Africa and thus are not true STP endemics. Outside of the TEA, STP ostracods show weak
567 biogeographic connectivity with other tropical Atlantic regions as indicated by the low number
568 of common species (Table 2; Fig. 9). In the west, the mid-Atlantic Barrier (deep and wide
569 Atlantic itself) effectively isolates the TEA from West Atlantic but is occasionally permeable
570 through the easterly flowing Equatorial Counter Currents (Floeter et al., 2008; Fajemila and
571 Langer, 2017). Indeed, there are many characteristic West Atlantic genera found in STP,
572 including *Neocaudites*, *Puriana*, and *Cativella* (Omatsola, 1972; Coimbra et al., 2004). The
573 STP ostracod is slightly more similar to the Southwestern Atlantic fauna at species level despite
574 the Northwestern Atlantic being much more speciose as a biodiversity hotspot, which is likely
575 due to the difference in geographic distance (~3500 km from the Brazil and ~8696 from the
576 Caribbean) (Da Costa et al., 2022). In the north, subtropical species from the Mediterranean
577 and Northwest African coast may be brought southward by the Canary Current and further
578 dispersed by the Gulf of Guinea Current (Le Lœuff and Von Cosel, 1998). STP ostracods
579 therefore hold certain similarity with the Northeastern Atlantic fauna. Interestingly, with the
580 major biogeographic barrier of the Benguela Current in the south, STP shares 11 species in
581 common with Zanzibar but only 3 with the Southwest African coast, for which there are three
582 possible explanations. First, foraminifera evidence shows that the Benguela barrier could be
583 breached when warm water Agulhas eddies pinched off into the South Atlantic during
584 interglacial (i.e., the Agulhas leakage hypothesis) (Gordon, 2003). Some amphisteginid
585 foraminifera from the warm WIO managed to colonize the Atlantic in this way, but their
586 populations in colder Southwest Africa became locally extinct during glacial intervals and
587 eventually only the TEA populations survived until today (Fajemila and Langer, 2017). We
588 suggest that ostracods may undergo similar processes in history. For example, *Kotoracythere*
589 *inconspicua* and *Keijia demissa* as two common species in STP and Zanzibar are known to
590 originate during late Miocene in the Indo-Pacific and display pan-tropical distributions today
591 (Sridhar et al., 2007; Coimbra et al., 1999). It is likely that they took the dispersal route from
592 the Indo-Pacific to TEA through South Africa, since the Tethyan Seaway had already been
593 closed by late Miocene. Second, some common species in STP and Zanzibar are Tethyan relicts,
594 *Paracytheridea tschoppi* for instance (Coimbra et al., 1999). This species dispersed into the
595 Atlantic and Indo-Pacific before the closure of the Tethyan Seaway and experienced a long
596 period of evolutionary stasis (Coimbra et al., 1999). Lastly, low faunal overlap between STP
597 and Southwest Africa could be caused by sampling bias, but the relatively large species pool of
598 the Southwest Africa province makes this explanation less plausible. In summary, although our
599 biogeographic study here is not corrected for uneven sampling efforts and patchy geographic
600 coverage in each province, it builds a reasonably solid basic framework of ostracod
601 provinciality in the tropical Atlantic. Ostracods have low dispersal capacity because they do not
602 have a planktic larvae stage, unlike foraminifera and many other benthic groups (Yasuhara et
603 al., 2017); yet some species still achieve transoceanic and even cosmopolitan distribution being
604 passively carried by floating algae, migratory birds, and vessels. The coexistence of wide-



605 ranging species together with many endemic species in the oceanic islands of STP invokes
606 further surveys to understand ostracod provinciality and dispersal vectors, in face of increasing
607 anthropogenic transport.

608

609 **5 Conclusion**

610 Our comparative study of meiobenthic faunas from STP and Zanzibar reveals the patterns and
611 determinants of these unique island ecosystems reflecting both universal ecological rules and
612 region-specific conditions. Diversity of each region largely mirrors the larger-scale patterns of
613 biogeographic provinces, with very high diversity on coral reefs in Zanzibar within the rich
614 WIO while uniformly low diversity across habitats in STP within the impoverished TEA.
615 Habitat type is the most important factor accounting for faunal variability within each region to
616 define basically the reefal and non-reefal assemblages, and algae coverage further impacts the
617 relative dominance of coral-affiliated, phytal, and bottom-dwelling taxa to subdivide these
618 assemblages. Ostracods and foraminifera as important members of meiobenthic community
619 show overall consistency in their diversity and composition patterns within and between regions.
620 However, minor differences are most probably explained by high ecological specialization and
621 habitat requirements of foraminifera, so that they have higher compositional changes across
622 environments and low diversity in transitional environments. Finally, STP ostracod fauna
623 seemingly shows high level of endemism in the isolated TEA province, but our understanding
624 of their large-scale biogeographic patterns and dispersal pathways is extremely deficient. We
625 appeal to future studies to investigate the diversity and distribution of ostracods on coral reefs
626 from larger geographic regions to fully explore the ecological and conservation significance of
627 these fascinating benthic organisms. At the same time, high endemism in STP emphasizes the
628 need for targeted conservation of these little-studied yet vulnerable island ecosystems.

629

630 **Data availability**

631 All data supporting this manuscript (ostracod and foraminifera census data; ostracod occurrence
632 data from tropical Atlantic) is included in the Supplement.

633

634 **Author contributions**

635 SYT and ML developed the concept. ML collected and samples. SYT carried out the
636 experiments and collected the data. SYT and CLW performed the data analyses. SYT drafted
637 the manuscript. ML, MY, and CLW reviewed and edited the manuscript.

638

639 **Competing interests**

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

641

642 **Acknowledgements**

643 We thank Ute Möller for her assistance in the laboratory.

644

645 **Financial support**



646 This research has been supported by the Alexander von Humboldt Research Fellowship (to
647 SYT) and the Deutsche Forschungsgemeinschaft (grant no. TI 1364/2-1, to SYT; grant no. LA
648 884/10-1, to ML); the Research Grants Council, University Grants Committee (grant nos. HKU
649 17306023 and G-HKU709/21, to MY); and the National Science and Technology Council
650 (grant no. NSTC 112-2611-M-002-011, to CLW).

651

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