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

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Abstract

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

1 Introduction

Near-shore oceanic islands are of particular ecological and conservation importance for their unique roles as dispersal nodes and reservoirs of marine benthic diversity (Cowie and Holland, 2006). The São Tomé–Príncipe Archipelago (STP) in the tropical East Atlantic (TEA) and the Zanzibar Archipelago in the western Indian Ocean (WIO) represent two such systems situated in western and eastern sides of equatorial Africa, respectively. They are in highly comparable geographic settings (i.e., close to the African continent at equatorial latitudes) and broadly similar environmental conditions (i.e., tropical shallow marine) (Da Costa et al., 2022; Tian et al., 2024a), which make them natural analogues for contrastive studies of marine diversity and community structure (Table 1 and Fig. 1). These archipelagos provide important offshore habitats and nursery areas for coastal and pelagic organisms (Da Costa et al., 2022). Isolated but not distant from the continent, they may support certain levels of endemism while maintaining connectivity with surrounding shelf ecosystems (Maia et al., 2018). As recipients and redistributors of tropical biotas via equatorial currents, these islands function as steppingstones to promote faunal exchange across biogeographic provinces (Cowie and Holland, 2006; Fajemila and Langer, 2017). At the same time, both the STP and Zanzibar ecosystems provide essential marine resources to local communities but face severe over-exploitation and habitat degradation, in conjunction with anthropogenic climate changes (Da Costa et al., 2022; Bravo et al., 2021).

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

	Region	Temperature °C	Salinity	Net primary productivity (mgC/m2/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

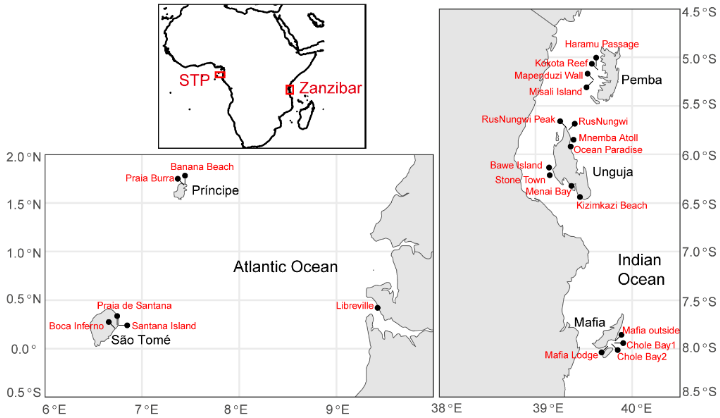

Fig. 1. Map showing the STP Archipelago in western Africa and the Zanzibar Archipelago in eastern Africa with ostracod sampling locations.

At a larger spatial scale of biogeographic province, the biotic and abiotic contexts of these two archipelagoes diverge sharply. The TEA is one of the least studied marine tropical provinces characterized by low biodiversity, high productivity, and pronounced endemism (Da Costa et al., 2022; Floeter et al., 2008; Polidoro et al., 2017). Environmentally, it is featured by complex hydroclimatic conditions. Cold boundary currents (Canary in the north and Benguela in the south) and seasonal upwelling along western African coast restrict the geographic range of true tropical regions (Da Costa et al., 2022; Polidoro et al., 2017). Biogeographically, the TEA has a long history of isolation with the opening of the Atlantic separating it from South America since early Jurassic; the closure of the Tethyan Seaway disconnecting it with Indo-Pacific realm during the Miocene; and finally, the establishment of the Benguela Current isolating it from southern Indian Ocean during the Pliocene (Floeter et al., 2008; Cowman et al., 2017). On the eastern side of tropical Africa, however, the western Indian Ocean (WIO) harbors a much richer shallow-marine fauna typical of coral reefs and reef-associated environments under the influence of warm Agulhas Current (Obura, 2012). The tropical section of the WIO exhibits a moderate level of endemism in the periphery of vast Indo-Pacific realm, with biogeographic affinity to both the Red Sea and central Indo-Pacific (Obura, 2012; Cowman et al., 2017). It is expected that the differences between the TEA and WIO at large regional scale should lead to idiosyncratic patterns in the diversity and composition of the STP versus Zanzibar faunas.

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

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

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2 Material and methods

2.1 Regional setting

The São Tomé-Príncipe Archipelago is located along the Cameroon Volcanic Line at 243 km off the continental West African coast in the Gulf of Guinea (Canterle et al., 2020) (Fig. 1; Table 1). It consists of two main islands, São Tomé and Príncipe, with a coastline extension of 185 km and total land area of 1042 km^2. Biogeographically, the archipelago is part of the Guinea Current Large Marine Ecosystem extending from Guinea Bissau to Angola within the Tropical East Atlantic (TEA) province (Fajemila and Langer, 2017). It is influenced by three incoming currents, namely the Gulf of Guinea Current from North, the Benguela Current from South, and the easterly flowing Equatorial Counter Current (Da Costa et al., 2022). The convergence of ocean currents causes seasonal equatorial upwelling and dominates regional productivity (Friedlander et al., 2014). Freshwater and particulate discharge from ~~main~~ rivers (Ogooué and Congo) leads to great ~~spatial-temporal~~ variations in salinity and turbidity in coastal waters (Friedlander et al., 2014). Steep environmental gradients occur across the upper water column, with temperature reaching typical tropical ranges of 25-29 °C at surface while dropping to ~20 °C below a constant thermocline at depths of 20-30 m, and likewise for salinity and nutrient content among other parameters (Maia et al., 2018). As constrained by regional hydrological conditions, no extensive matrix of true coral reefs exists in the Gulf of Guinea including STP, instead the benthic habitats are characterized by a mosaic of scattered rocky reefs colonized by various hard corals, turf algae, macroalgae, and sponges (Otero-Ferrer et al., 2020). Mangroves and seagrass beds are the other two major habitats along the islands' coast. In terms of substratum, a large proportion of the coastal area is covered by dark-colored volcanic sands in contrast to stable quartz sands and calcareous bioclastic sands.

The Zanzibar Archipelago is situated 49 km away from the Tanzania mainland along the East African coast (Narayan et al., 2022) (Fig. 1; Table 1). The three main islands, Pemba, Unguja, and Mafia measure a total land area of 3002 km^2 and a coastline of 767 km. The archipelago belongs to the Somali Coastal Current Large Marine Ecosystem that stretches from Somalia to the northeastern coast of South Africa in the western Indian Ocean (WIO) province (Thissen and Langer, 2017). Major currents influencing this region include the westward-flowing South Equatorial Current and the northward-flowing East African Coastal Current (Tian et al., 2024a). The tropical monsoonal climate regulates annual temperature variation between 25-29 °C with humid and dry seasons (Narayan et al., 2022). The Zanzibar islands possess one of the largest reef areas along the coast of East Africa, but many local reefs are in early-middle stages of degradation because of increasing marine pollution and urbanization, especially in heavily populated Stone Town areas (Grimsditch et al., 2009; Bravo et al., 2021; Larsen et al., 2023). Shallow fringing reefs and deep fore reefs are the most common habitat, followed by vegetated sand flats and mangroves. The substratum is primarily calcareous bioclastic sands in fine to medium grain size with varying amounts of reef rubble, or otherwise fine quartz sands.

2.2 Sample processing and data integration

In total ten surface sediment samples were collected from the ~~Sao Tome and Principe~~ islands in addition to one sample along continental coast in Libreville directly east of the archipelago (Fig. 1). These samples cover a depth range of 0.5-30 m across the tidal and subtidal zones and represent the habitat types of marginal fringing reefs, sand flats, and mangroves. Samples were collected by scuba diving to scrape along the seabed and fill plastic containers with top 2 cm of the surface sediments, in order to avoid the loss of finer particles due to suspension. In the laboratory, sediments were washed through a 63 µm sieve, oven dried at 50 °C, and dry sieved over a 150 µm mesh sieve. Subfossil ostracods were picked from the > 150 µm size fraction and a single valve or a carapace was treated as one individual, which is the standard method in ostracod research (Tian et al., 2024a). Specimens preserved with soft parts (live) were counted together with the empty ones (dead) to make up the total, time-averaged assemblage, which is proven to effectively define benthic habitats (Tian et al., 2024a). In the next step, we integrated the census count of STP ostracods with previously published ostracod data from Zanzibar after rigorous taxonomic standardization (Tian et al., 2024a). Published foraminifera data from the two regions were integrated in the same way so that we build a trans-regional, multi-proxy, large-size dataset of benthic meiofaunas (Thissen and Langer, 2017; Fajemila and Langer, 2017).

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

Table 2. Definitions of tropical-subtropical biogeographic provinces of the Atlantic Ocean (Le Lœuff and Von Cosel, 1998; Floeter et al., 2008) and shared number of species with STP. See 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

2.3 Quantitative analyses

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

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

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

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

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

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

3 Results

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

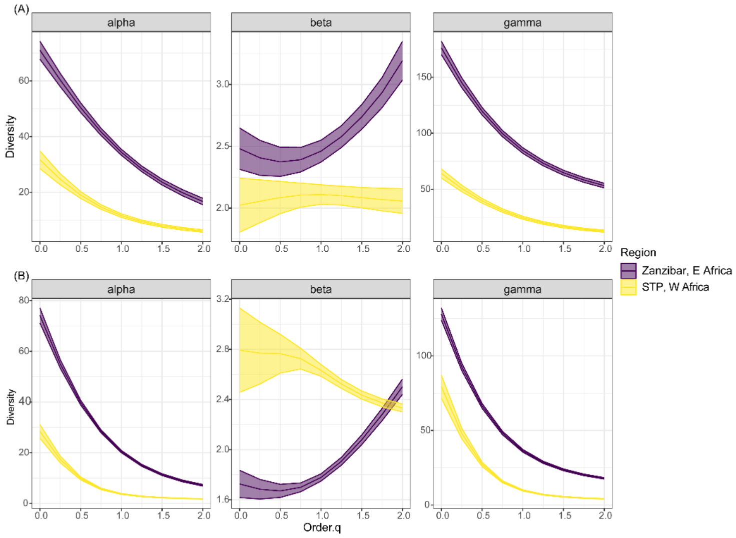

Fig. 2. Alpha, beta, and gamma diversity of the STP and Zanzibar regions for ostracods (A) and foraminifera (B) shown by Hill number profiles. Standardized sample coverage: ostracod 82.5% for alpha and beta, 96.7% for gamma; foraminifera 97.3% for alpha and beta, 98.9% for gamma. The shaded area shows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

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

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

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

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

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

Table 3. Environmental controls of ostracod and foraminifera alpha diversity (q=1) in Zanzibar. Statistics from GAMM modelling showing the significant parameters in the averaged top model. 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

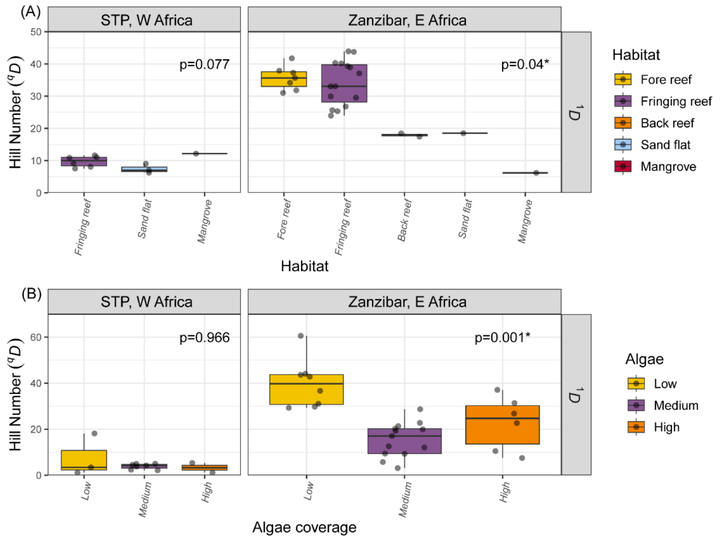

Fig. 5. Box plots showing variations in ostracod alpha diversity between habitat types (A) and foraminifera alpha diversity between algae coverage levels (B) for order q=1 in STP and Zanzibar regions. p-value given by the Kruskal-Wallis test.

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

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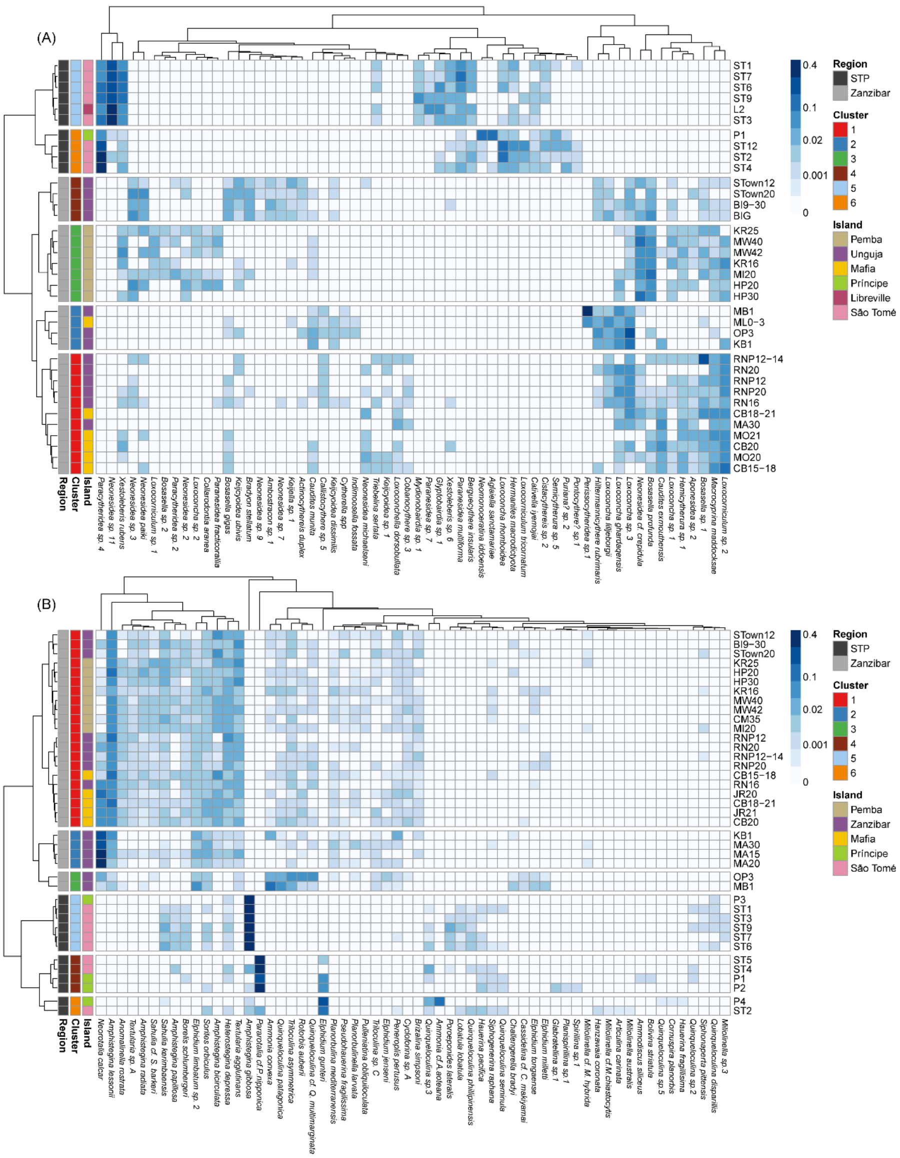

Fig. 6. Composition of ostracod (A) and foraminifera (B) assemblages in STP and Zanzibar in terms of the top 10 indicator species of each cluster at order *q*=1. The blue heatmaps illustrate species count in each sample after applying a fourth root transformation. Dendrograms based on Horn dissimilarity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

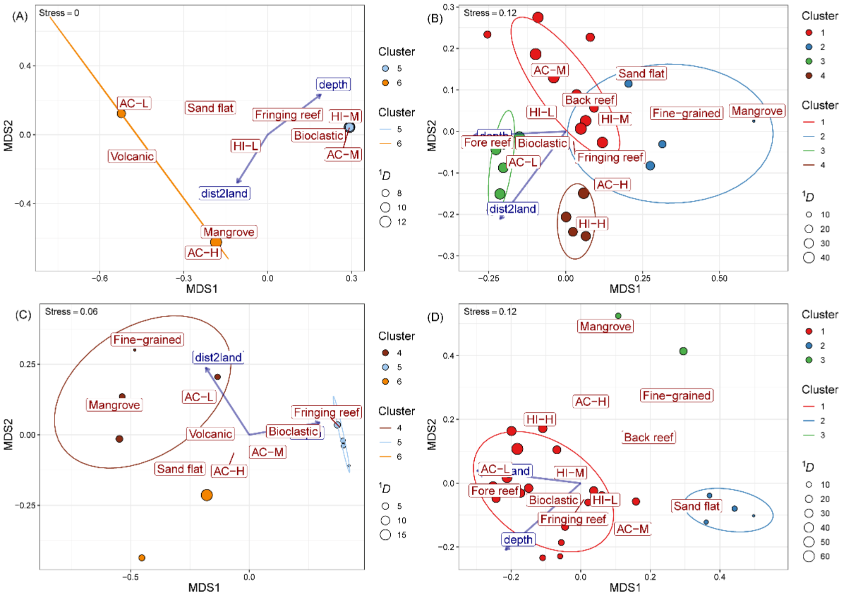

Fig. 7. nMDS ordination showing faunal variation correlated with environmental factors in each region for each organism. (A) STP ostracods; (B) Zanzibar ostracods; (C) STP foraminifera; (D) Zanzibar foraminifera. The vectors indicate correlations with continuous environmental variables and labels indicate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

Table 4. Environmental controls of ostracod and foraminifera faunal composition (q=1) in 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**

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

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

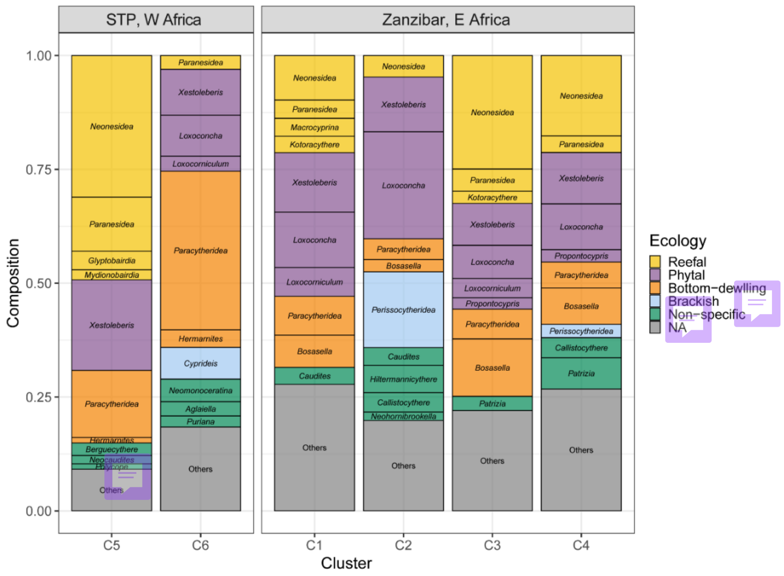

Fig. 8. Proportional composition of ostracod clusters at order q=1 with ecological groups shown by colors. The top 10 genera of highest mean relative abundance in each cluster are assigned to one of the ecological groups, i.e., reefal, phytal, bottom-dwelling, brackish, or non-specific. All genera other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

Our biogeographic investigation indicates that the ostracod fauna in STP has potentially a high level of endemism within and beyond the TEA province (Table 2; Fig. 9; Table S4). There are 22 species in STP shared with tropical continental areas of west Africa, the Gulf of Guinea in particular. The biogeographic connections of STP with all other Atlantic provinces are much weaker, i.e., 7 species in common with the Northwestern and Northeastern Atlantic, 8 species with the Southwestern Atlantic, and only 3 species with the Southeastern Atlantic. The STP and Zanzibar faunas in our dataset overlap with 11 ostracod species and 16 foraminifera species, on the other hand.

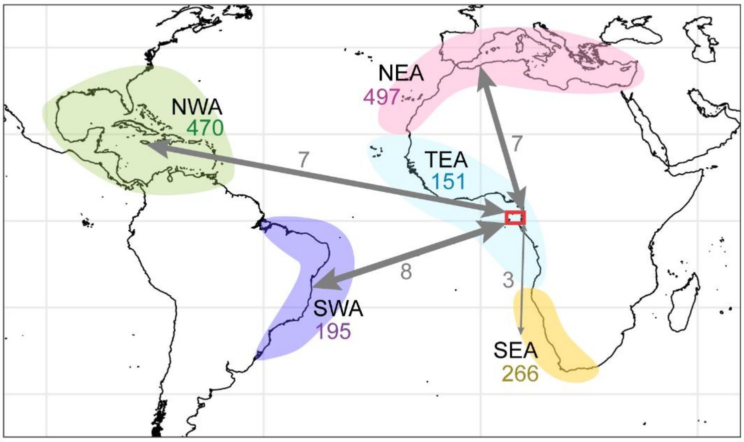

Fig. 9. Schematic map showing the biogeographic relationship of STP with tropical-subtropical Atlantic provinces. Each colored number indicates the number of species described in each province. Thickness of the arrow with number over it indicates connectivity by the number of common species. Red box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

4 Discussion

4.1 Impoverishment of the STP fauna in the TEA province

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

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

4.2 Environmental control of local diversity and faunal composition

The GAMM modelling reveals that environmental effects on local diversity vary between ~~two~~ organisms and between ~~two~~ regions (Table 3). In Zanzibar, ostracod local diversity is regulated by habitat type as the fore and fringing reefs with high topographic complexity support more diverse assemblages compared to marginal reefs, mangroves, and featureless soft bottom habitats (Fig. 5A). Diversity is particularly high on some fringing reefs with medium algae coverage (e.g., RNs and CBs) (Fig. 3A), likely because interlaced hard corals, macro algae, and turf algae offer diverse and heterogenous microhabitats to accommodate different ecological groups (Tian et al., 2024a). It is intriguing that the local diversity of foraminifera in Zanzibar responds nonlinearly to the algae ~~factor~~ with the lowest diversity at medium coverage (e.g., MAs and RNPs) (Figs. 4A and 5B). In fact, many sites with medium algae coverage can be characterized as transitional environments between hard and soft bottoms, where the sediments are homogenous, medium-grained bioclastic sands. These sites are idiosyncratic ~~in terms of not only diversity~~ but also composition (e.g., the MAs form its own foraminifera cluster C2) (Fig. 6B). Neither reefal nor phytal foraminifera flourish in such environments, so that local diversity records the lowest level. This is in sharp contrast to the ostracod pattern that various ecological groups overlap in algae-covered reefal habitats to achieve high diversity, which conforms to the classic intermediate disturbance hypothesis (Viljur et al., 2022; Townsend et al., 1997). A possible explanation for foraminifera being a contrarian in this regard is that they may have high ecological specialization and specific habitat requirements, which make them avoid transitional algae-covered environments. Then, in STP, the local diversity of both groups does not evidently follow any environmental regulations tested (Fig. 5). Diversity distribution is essentially uniform for ostracods while site-specific for foraminifera. As the seascape is predominantly sandy and muddy bottoms along the west African coast (Friedlander et al., 2014), small fringing reefs in STP may provide one of the few hard substrates in this region for reef organisms yet they lack the topographic complexity required to host high diversity like true tropical coral reef ecosystems. Consequently, there are no locally diverse benthic assemblages in STP.

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

Despite distinct taxonomic compositions of the STP and Zanzibar faunas at species and even genus level, there is a marked inter-regional convergence in the ecological structure of ostracod reefal and non-reefal assemblages in terms of the proportions of coral, phytal, bottom-dwelling, and euryhaline taxa (Fig. 8). The fringing reef cluster (C5) in STP and pristine fore reef cluster (C3) in Zanzibar both show highest abundance of coral affiliated taxa, while the other two reefal clusters with algae cover (C1 and C4) in Zanzibar have comparatively more phytal taxa besides coral taxa. Regarding the non-reefal clusters, C6 in STP is dominated by bottom-dwelling and secondarily phytal taxa, in addition to a small proportion of euryhaline and almost no coral taxa. C2 in Zanzibar is instead comprised of primarily phytal taxa followed by euryhaline and lastly bottom-dwelling taxa. The discrepancy between non-reefal clusters C6 and C2 is likely caused by low vegetation coverage in the sand flat habitats in STP, where sea floor is mostly bare, so that the bottom-dwelling taxa thrive while the phytal taxa ~~perish.~~ The exclusive occurrence of euryhaline taxa in the non-reefal intertidal clusters indicates salinity variations there, in contrast to normal marine conditions in deeper subtidal environments. Our trans-regional comparison clearly demonstrates a persistent correspondence between ostracod ecological structure and environmental character. Specifically, the relative abundances of coral-affiliated, phytal, and bottom-dwelling taxa seem to vary predictably along a benthic community gradient depending on the percentage coverage of hard corals, algae and bare sands. Although more studies from other regions are imperative to test the generality of this pattern, the findings presented here are considered illuminating. Ostracods can potentially be an indicator of reef condition to track the degradation from coral- to algae-dominated states (Tian et al., 2024a), if a quantitative correlation is established between ostracod ecological composition and benthic community in tropical reefs and reef-associated habitats.

4.3 Biogeography of STP ostracods

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

5 Conclusion

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

Data availability

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

Author contributions

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

Competing interests

The authors declare that they have no conflict of interest.

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References

Anderson, D. R., Burnham, K. P., and Thompson, W. L.: Null hypothesis testing: problems, prevalence, and an alternative, The journal of wildlife management, 912-923, https://doi.org/10.2307/3803199, 2000.

Baldrighi, E. and Manini, E.: Deep-sea meiofauna and macrofauna diversity and functional diversity: are they related?, Marine Biodiversity, 45, 469-488, https://doi.org/10.1007/s12526-015-0333-9, 2015.

Bellwood, D. R., Renema, W., and Rosen, B. R.: Biodiversity hotspots, evolution and coral reef biogeography, in: Biotic Evolution and Environmental Change in Southeast Asia, Cambridge University Press, Cambridge, 216-245, https://doi.org/10.1017/CBO9780511735882.011, 2012.

Bravo, H., Cannicci, S., Huyghe, F., Leermakers, M., Sheikh, M. A., and Kochzius, M.: Ecological health of coral reefs in Zanzibar, Reg. Stud. Mar. Sci., 48, 102014, https://doi.org/10.1016/j.rsma.2021.102014, 2021.

Cáceres, M. D. and Legendre, P.: Associations between species and groups of sites: indices and statistical inference, Ecology, 90, 3566-3574, https://doi.org/10.1890/08-1823.1, 2009.

Canterle, A. M., Nunes, L. T., Fontoura, L., Maia, H. A., and Floeter, S. R.: Reef microhabitats mediate fish feeding intensity and agonistic interactions at Príncipe Island Biosphere Reserve, Tropical Eastern Atlantic, Mar. Ecol., 41, e12609, https://doi.org/10.1111/maec.12609, 2020.

Carvalho, I., Pereira, A., Martinho, F., Vieira, N., Brito, C., Guedes, M., and Loloum, B.: Cetaceans of São Tomé and Príncipe, in: Biodiversity of the Gulf of Guinea Oceanic Islands, edited by: Luis M. P. Ceríaco, R. F. d. L., Martim Melo, Rayna C. Bell, Springer, 621-641, 2022.

Chao, A. and Ricotta, C.: Quantifying evenness and linking it to diversity, beta diversity, and similarity, Ecology, 100, e02852, https://doi.org/10.1002/ecy.2852, 2019.

Chao, A., Chiu, C.-H., and Jost, L.: Unifying species diversity, phylogenetic diversity, functional diversity, and related similarity and differentiation measures through Hill numbers, Annu. Rev. Ecol. Evol. Syst., 45, 297-324, https://doi.org/10.1146/annurev-ecolsys-120213-091540, 2014a.

Chao, A., Gotelli, N. J., Hsieh, T., Sander, E. L., Ma, K., Colwell, R. K., and Ellison, A. M.: Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies, Ecol. Monogr., 84, 45-67, https://doi.org/10.1890/13-0133.1, 2014b.

Chao, A., Thorn, S., Chiu, C. H., Moyes, F., Hu, K. H., Chazdon, R. L., Wu, J., Magnago, L. F. S., Dornelas, M., and Zelený, D.: Rarefaction and extrapolation with beta diversity under a framework of H ill numbers: The iNEXT. beta3D standardization, Ecol. Monogr., 93, e1588, https://doi.org/10.1002/ecm.1588, 2023.

Coimbra, J. C., Pinto, I. D., Wurdig, N. L., and do Carmo, D. A.: Zoogeography of Holocene Podocopina (Ostracoda) from the Brazilian equatorial shelf, Mar. Micropaleontol., 37, 365-379, https://doi.org/10.1016/S0377-8398(99)00025-0, 1999.

Coimbra, J. C., Ramos, M. I. F., Whatley, R. C., and Bergue, C. T.: The taxonomy and zoogeography of the family Trachyleberididae (Crustacea: Ostracoda) from the Equatorial Continental Shelf of Brazil, J. Micropalaeontol., 23, 107-118, https://doi.org/10.1144/jm.23.2.107, 2004.

Cowie, R. H. and Holland, B. S.: Dispersal is fundamental to biogeography and the evolution of biodiversity on oceanic islands, J. Biogeogr., 33, 193-198, https://doi.org/10.1111/j.1365-2699.2005.01383.x, 2006.

Cowman, P. F., Parravicini, V., Kulbicki, M., and Floeter, S. R.: The biogeography of tropical reef fishes: endemism and provinciality through time, Biol. Rev., 92, 2112-2130, https://doi.org/10.1111/brv.12323, 2017.

da Costa, L. M., Maia, H. A., and Almeida, A. J.: The fishes of the Gulf of Guinea oceanic islands, in: Biodiversity of the Gulf of Guinea Oceanic Islands: Science and Conservation. Cham: Springer International Publishing, edited by: Luis M. P. Ceríaco, R. F. d. L., Martim Melo, Rayna C. Bell, Springer, 431-478, 2022.

DeVantier, L., Turak, E., and Szava-Kovats, R.: Species richness and abundance of reef-building corals in the Indo-West Pacific: The local–regional relation revisited, Frontiers in Marine Science, 7, 487, https://doi.org/10.3389/fmars.2020.00487, 2020.

Dufrêne, M. and Legendre, P.: Species assemblages and indicator species: the need for a flexible asymmetrical approach, Ecol. Monogr., 67, 345-366, https://doi.org/10.1890/0012-9615(1997)067[0345:SAAIST]2.0.CO;2, 1997.

Fajemila, O. T. and Langer, M. R.: Spatial distribution and biogeographic significance of foraminiferal assemblages from Sao Tomé and Príncipe, Gulf of Guinea, West Africa, Neues Jahrbuch fur Geologie und Palaontologie-Abhandlungen, 285, 337-360, https://doi.org/10.1127/njgpa/2017/0686, 2017.

Ferreira-Airaud, B., Schmitt, V., Vieira, S., Rio, M. J. d. C. d., Neto, E., and Pereira, J.: The sea turtles of São Tomé and Príncipe: diversity, distribution, and conservation status, in: Biodiversity of the Gulf of Guinea Oceanic Islands: Science and conservation, edited by: Luis M. P. Ceríaco, R. F. d. L., Martim Melo, Rayna C. Bell, Springer, 535-553, 2022.

Floeter, S. R., Rocha, L. A., Robertson, D. R., Joyeux, J., Smith-Vaniz, W. F., Wirtz, P., Edwards, A. J., Barreiros, J. P., Ferreira, C. E., and Gasparini, J. L.: Atlantic reef fish biogeography and evolution, J. Biogeogr., 35, 22-47, https://doi.org/10.1111/j.1365-2699.2007.01790.x, 2008.

Friedlander, A. M., Ballesteros, E., Fay, M., and Sala, E.: Marine communities on oil platforms in Gabon, West Africa: high biodiversity oases in a low biodiversity environment, PLoS One, 9, e103709, https://doi.org/10.1371/journal.pone.0103709, 2014.

Gordon, A. L.: The brawniest retroflection, Nature, 421, 904-905, https://doi.org/10.1038/421904a, 2003.

Grimsditch, G. D., Tamelander, J., Mwaura, J., Zavagli, M., Takata, Y., and Gomez, T.: Coral reef resilience assessment of the Pemba channel conservation area, Tanzania, IUCN2009.

Hong, Y., Yasuhara, M., Iwatani, H., Harnik, P. G., Chao, A., Cybulski, J. D., Liu, Y., Ruan, Y., Li, X., and Wei, C.-L.: Benthic ostracod diversity and biogeography in an urbanized seascape, Mar. Micropaleontol., 174, 102067, https://doi.org/10.1016/j.marmicro.2021.102067 2022.

Kamiya, T.: Morphological and ethological adaptations of Ostracoda to microhabitats in Zostera beds, Dev. Palaeontol. Stratigr., 11, 303-318, https://doi.org/10.1016/S0920-5446(08)70191-2, 1988.

Keyser, D.: Ecology and zoogeography of recent brackish-water ostracoda (Crustacea) from south-west Florida, in: Aspects of ecology and zoogeography of recent and fossil Ostracoda, 207-222, 1977.

Keyser, D. and Mohammed, M.: Taxonomy of recent shallow marine Ostracods from Al-Hudeida City-Yemen, Mar. Micropaleontol., 164, 101974, https://doi.org/10.1016/j.marmicro.2021.101974, 2021.

Larsen, J., Maar, M., Rasmussen, M. L., Hansen, L. B., Hamad, I. Y., and Stæhr, P. A. U.: High-resolution hydrodynamics of coral reefs and tracing of pollutants from hotel areas along the west coast of Unguja Island, Zanzibar, Mar. Pollut. Bull., 191, 114968, https://doi.org/10.1016/j.marpolbul.2023.114968, 2023.

Le Lœuff, P. and von Cosel, R.: Biodiversity patterns of the marine benthic fauna on the Atlantic coast of tropical Africa in relation to hydroclimatic conditions and paleogeographic events, Acta Oecol., 19, 309-321, https://doi.org/10.1016/S1146-609X(98)80035-0, 1998.

Leray, M. and Knowlton, N.: DNA barcoding and metabarcoding of standardized samples reveal patterns of marine benthic diversity, Proc. Natl. Acad. Sci. USA., 112, 2076-2081, https://doi.org/10.1073/pnas.1424997112, 2015.

Losos, J. B. and Schluter, D.: Analysis of an evolutionary species–area relationship, Nature, 408, 847-850, https://doi.org/10.1038/35048558, 2000.

Maia, H. A., Morais, R. A., Quimbayo, J. P., Dias, M. S., Sampaio, C. L., Horta, P. A., Ferreira, C. E. L., and Floeter, S. R.: Spatial patterns and drivers of fish and benthic reef communities at

São Tomé Island, Tropical Eastern Atlantic, Mar. Ecol., 39, e12520, https://doi.org/10.1111/maec.12520, 2018.

Mamo, B. L., Cybulski, J. D., Hong, Y., Harnik, P. G., Chao, A., Tsujimoto, A., Wei, C.-L., Baker, D. M., and Yasuhara, M.: Modern biogeography of benthic foraminifera in an urbanized tropical marine ecosystem, Geological Society, London, Special Publications, 529, SP529-2022-2175, https://doi.org/10.1144/SP529-2022-175, 2023.

Narayan, G. R., Herrán, N., Reymond, C. E., Shaghude, Y. W., and Westphal, H.: Local Persistence of Large Benthic Foraminifera (LBF) under Increasing Urban Development: A Case Study from Zanzibar (Unguja), East Africa, J. Earth Sci., 33, 1434-1450, https://doi.org/10.1007/s12583-022-1702-5, 2022.

Obura, D.: The diversity and biogeography of Western Indian Ocean reef-building corals, PLOS ONE, e45013, https://doi.org/10.1371/journal.pone.0045013, 2012.

Omatsola, M. E.: Recent and subrecent Trachyleberididae and Hemicytheridae (Ostr., Crust) from the Western Niger Delta, Nigeria, Bull. geol. lnstn Univ. Upsala, 3, 37-120, 1972.

Otero-Ferrer, F., Tuya, F., Bosch Guerra, N. E., Herrero-Barrencua, A., Abreu, A., and Haroun, R.: Composition, structure and diversity of fish assemblages across seascape types at Príncipe, an understudied tropical island in the Gulf of Guinea (eastern Atlantic Ocean), Afr. J. Mar. Sci., 42, 381-391, https://doi.org/10.2989/1814232X.2020.1826358, 2020.

Polidoro, B. A., Ralph, G. M., Strongin, K., Harvey, M., Carpenter, K. E., Arnold, R., Buchanan, J. R., Camara, K. M. A., Collette, B. B., and Comeros-Raynal, M. T.: The status of marine biodiversity in the Eastern Central Atlantic (West and Central Africa), Aquat. Conserv.: Mar. Freshwat. Ecosyst., 27, 1021-1034, https://doi.org/10.1002/aqc.2744, 2017.

Porriños, G., Metcalfe, K., Nuno, A., da Graça, M., Walker, K., Dixon, A., Guedes, M., Nazaré, L., Dos Santos, A., and Colman, L. P.: Fish community composition in the tropical archipelago of São Tomé and Príncipe, PloS one, 19, e0312849, https://doi.org/10.1371/journal.pone.0312849, 2024.

Prazeres, M. and Renema, W.: Evolutionary significance of the microbial assemblages of large benthic Foraminifera, Biol. Rev., 94, 828-848, https://doi.org/10.1111/brv.12482, 2019.

Purper, I. and de Orenellas, L. P.: The genus *Paracytheridea* (Ostracoda) in the northern/northwestern Brazilian continental shelf, Pesquisas em Geociências, 20, 103-124, https://doi.org/10.22456/1807-9806.21675, 1987.

Reagan, J. R., Seidov, D., Wang, Z., Dukhovskoy, D., Boyer, T. P., Locarnini, R. A., Baranova, O. K., Mishonov, A. V., Garcia, H. E., and Bouchard, C.: World ocean atlas 2023 [dataset], 2024.

RStudio, T.: RStudio: Integrated development for R [Computer software]. Boston, MA: RStudio, Inc, 2016.

Sridhar, S., Hussain, S., Periakali, P., and Kumar, V.: Ostracod *Kotoracythere inconspicua* (Brady) from the Palk Bay, off Rameswaram, Southeast Coast of India: Its Zoogeography and Ecology, Journal Geological Society of India, 70, 981-986, 2007.

Thissen, J. and Langer, M.: Spatial Patterns and Structural Composition of Foraminiferal Assemblages from the Zanzibar Archipelago (Tanzania), Palaeontographica Abteilung A, 308, 1-67, https://doi.org/10.1127/pala/308/2017/1, 2017.

Tian, S. Y., Langer, M., Yasuhara, M., and Wei, C.-L.: Reefal ostracod assemblages from the Zanzibar Archipelago (Tanzania), Biogeosciences, 21, 3523-3536, https://doi.org/10.5194/bg-21-3523-2024, 2024a.

Tian, S. Y., Yasuhara, M., Condamine, F. L., Huang, H.-H. M., Fernando, A. G. S., Aguilar, Y. M., Pandita, H., Irizuki, T., Iwatani, H., Shin, C. P., Renema, W., and Kase, T.: Cenozoic history of the tropical marine biodiversity hotspot, Nature, 632, 343–349, https://doi.org/10.1038/s41586-024-07617-4, 2024b.

Tittensor, D. P., Mora, C., Jetz, W., Lotze, H. K., Ricard, D., Berghe, E. V., and Worm, B.: Global patterns and predictors of marine biodiversity across taxa, Nature, 466, 1098, https://doi.org/10.1038/nature09329, 2010.

Titterton, R. and Whatley, R.: Recent Bairdiinae (Crustacea, Ostracoda) from the Solomon Islands, J. Micropalaeontol., 7, 111-142, https://doi.org/10.1144/jm.7.2.111, 1988.

Townsend, C. R., Scarsbrook, M. R., and Dolédec, S.: The intermediate disturbance hypothesis, refugia, and biodiversity in streams, Limnol. Oceanogr., 42, 938-949, https://doi.org/10.4319/lo.1997.42.5.0938, 1997.

Tuya, F., Herrero-Barrencua, A., Bosch, N., Abreu, A., and Haroun, R.: Reef fish at a remote tropical island (Principe Island, Gulf of Guinea): disentangling taxonomic, functional and phylogenetic diversity patterns with depth, Marine and Freshwater Research, 69, 395-402, https://doi.org/10.1071/MF17233, 2017.

Viljur, M. L., Abella, S. R., Adámek, M., Alencar, J. B. R., Barber, N. A., Beudert, B., Burkle, L. A., Cagnolo, L., Campos, B. R., and Chao, A.: The effect of natural disturbances on forest biodiversity: an ecological synthesis, Biol. Rev., 97, 1930-1947, https://doi.org/10.1111/brv.12876, 2022.

Whatley, R. C. and Watson, K.: A preliminary account of the distribution of Ostracoda in recent reef and reef associated environments in the Pulau Seribu or Thousand Island Group, Java Sea, Dev. Palaeontol. Stratigr., 11, 399-411, https://doi.org/10.1016/S0920-5446(08)70197-3, 1988.

Witman, J. D., Etter, R. J., and Smith, F.: The relationship between regional and local species diversity in marine benthic communities: a global perspective, Proc. Natl. Acad. Sci. USA., 101, 15664-15669, https://doi.org/10.1073/pnas.0404300101, 2004.

Wood, S. N.: Generalized additive models, Annual Review of Statistics and its Application, 12, 497-526, https://doi.org/10.1146/annurev-statistics-112723-034249, 2024.

Wouters, K.: On the modern distribution of the euryhaline species *Cyprideis torosa* (Jones, 1850)(Crustacea, Ostracoda), J. Micropalaeontol., 36, 21-30, https://doi.org/10.6084/m9.figshare.c.3149791.v1, 2017.

Yasuhara, M., Tittensor, D. P., Hillebrand, H., and Worm, B.: Combining marine macroecology and palaeoecology in understanding biodiversity: microfossils as a model, Biol. Rev., 92, 199-215, https://doi.org/10.1111/brv.12223, 2017.