MS No. EGUSPHERE-2026-775

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

Dear editor and reviewers,

Here we are responding to the reviewers' comments on our manuscript No. EGUSPHERE-2026-775. We appreciate your positive evaluations and give us an opportunity to re-submit our MS. Here we addressed all the comments from two reviewers in the revised MS, and point-by-point responses are shown below.

Comments from the Reviewer#1 Olga Koukousioura:

This manuscript presents a high-quality and methodologically rigorous comparative analysis of benthic meiofaunal diversity, specifically focusing on Ostracoda and Foraminifera across the São Tomé-Príncipe (STP) (eastern Atlantic) and Zanzibar archipelagos (western Indian Ocean). Using a combination of standardized sampling and advanced statistical modeling (Hill numbers and GAMMs), the authors investigate how regional biogeography and local environmental drivers (e.g., coral cover, algae, and substrate type) influence community structure. The study highlights a stark "diversity disparity," with Zanzibar exhibiting significantly higher richness and more complex environmental partitioning compared to the relatively depauperate and homogeneous fauna of STP.

As the first comprehensive island-scale survey of ostracods for STP, the study fills a critical void in our understanding of tropical East Atlantic biodiversity and provides a holistic view of the "meiofaunal bottleneck" by comparing metazoan and protist responses to dispersal filters. The use of Hill numbers (effective number of species) is excellent for comparing datasets with varying sample sizes. The integration of Generalized Additive Mixed-effect Models (GAMM) effectively disentangles the relative contributions of environmental variables.

Zanzibar's alpha and gamma diversity are more than twice that of STP, reflecting the broader "species-rich" nature of the Indo-Pacific vs. the isolated Atlantic. In Zanzibar, habitat heterogeneity (reefal vs. non-reefal) is the primary driver of community assembly. In STP, the fauna is largely homogeneous across different benthic covers, suggesting that isolation and regional filters override local environmental selection.

The high endemism in STP ostracods suggests that the archipelago acts more as a biogeographic "cul-de-sac" rather than a stepping stone, due to the efficiency of the Mid-Atlantic Barrier. Could you elaborate on this?

Response: We appreciate your positive and constructive comments. To emphasize the STP as a "cul-de-sac", we added one summarizing sentence at Line 622 as follows:

"An exceedingly high level of endemism underscores the predominant role of STP as a

diversity reservoir instead of a steppingstone, as the soft and hard barriers strongly inhibit dispersal in all directions."

Suggestions for improvements

While the diversity indices are robust, the manuscript could benefit from a more detailed discussion on the specific functional traits of the endemic species found in STP.

Response: We thank the reviewer for this illuminating idea, but we do not observe that the endemic species present distinct functional traits compared to common, wide-spread species. As shown in Fig. 8 and corresponding paragraphs, the reefal ostracod assemblages in STP and Zanzibar have highly similar ecological composition in terms of the relative proportions of reefal, phytal, bottom-dwelling taxa, and the same is true for non-reefal assemblages in two regions. The endemic species are taxonomically distinct, but we have no evidence to suggest that they perform much different functions in the benthic ecosystem. In other words, the functional and ecological structure of ostracod assemblages are not dependent on the level of endemism. In a forthcoming taxonomic paper, we will systematically describe the endemic species found in STP.

The reliance on visual benthic cover (algae/coral/sand) is useful, but the absence of physical-chemical data (e.g., precise salinity) limits the ability to explain some of the "unexplained variance" in foraminiferal distributions. Are those data available?

Response: This is a very good point. Unfortunately, precise measurements of per-site environmental data are currently unavailable for the study region. Global databases of oceanic environmental data typically have low spatial resolution (e.g., 0.25° for the World Ocean Atlas), which is too coarse to be used in a regional study like the present one. Sample sites from one island are often recorded with highly similar and even completely the same environmental data in terms of temperature, salinity, and so on. Therefore, such data does not explain the faunal variances. In addition, there has been no regional, long-term monitoring program of water quality conducted by local authorities. Finally, we did not take on-site measurements of the environmental parameters due to the limitations of field campaign. Even if we took a one-off measurement at the time of sample collection, it would not reflect the annual mean or seasonal variations in environmental conditions. Last but not least, to account for local-scale variations in diversity and faunal compositions within a region, it is suggested that the local habitat factor may be much more important than the large-scale environmental variables (for example, see Ford and Roberts (2018)).

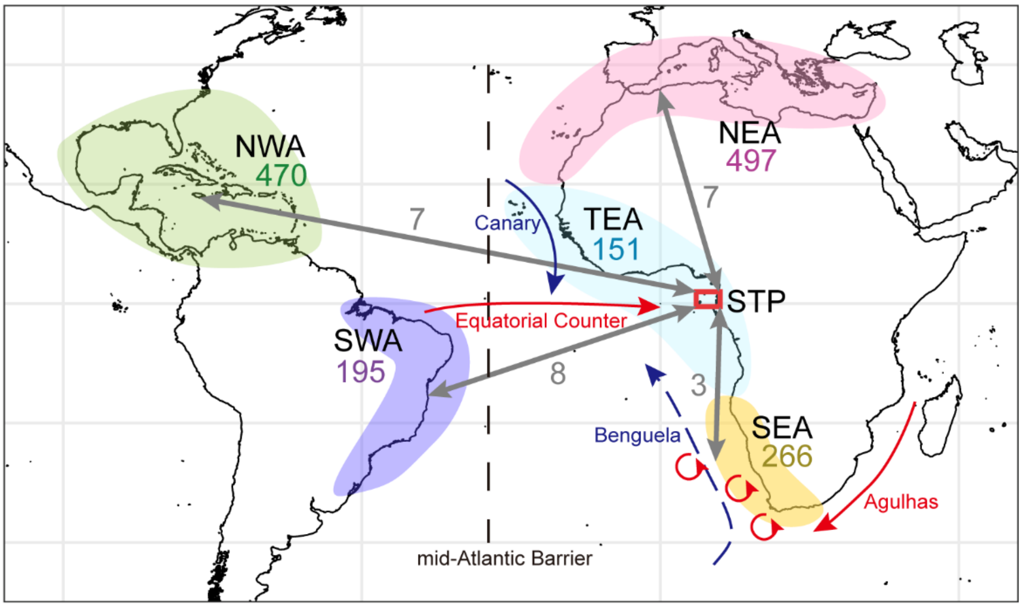
The results show that foraminiferal evenness in Zanzibar follows a "more obscure pattern" than ostracods. The authors should hypothesize whether this is due to different dispersal capabilities or a higher sensitivity to micro-scale environmental fluctuations not captured in the current model.

Response: We think that the uneven foraminifera assemblages are due to the over-dominance of a few opportunistic species in transitional environments. We revised the sentence at Line 527 as follows to elaborate on this:

“These sites are idiosyncratic in terms of not only diversity but also composition (e.g., the MAs form its own foraminifera cluster C2 and have very low evenness) (Fig. 6B). Neither reefal nor phytal foraminifera flourish in such environments and the assemblages are dominated by a few opportunistic species, so that local diversity records the lowest level.”

While the GAMM plots are informative, a simplified schematic showing the "Environmental Filtering Model" vs. the "Biogeographic Isolation Model" would help summarize the key findings for a broader audience.

Response: We included the GAMM results in Table 3 to show that ostracod local diversity is controlled by habitat topography while foraminifera local diversity is controlled by algae coverage. The biogeographic factor is not involved. We can only assume that the reviewer refers to section 4.3 and Fig. 9 about the biogeographic status of the STP ostracods. We accordingly modified Fig. 9 to add the ocean currents and dispersal barriers to illustrate the biogeographic relationship between STP and other provinces. We hope this helps with understanding.



Are the species names in the appendices cross-referenced with updated WoRMS (World Register of Marine Species) databases, particularly for the endemic STP taxa.

Response: We updated the species names with WoRMS.

This manuscript is a high-quality contribution to tropical marine biology and biogeography. The data is sound, and the conclusions are supported by robust statistical evidence. I recommend minor revisions to address the depth of the ecological discussion regarding foraminiferal patterns and further contextualization of the Atlantic results.

Response: We highly appreciate your recognition.

Comments from the Reviewer#2 Marie-Béatrice Forel:

Dear editors, dear colleagues,

I have been requested to review the manuscript entitledHeterogeneity of tropical diversity and ecosystems: reefal meiofaunas in equatorial western and eastern African islands submitted for publication to EGUsphere (manuscript: egusphere-2026-775).

The manuscript analyses the diversity and distribution of two meiofaunal groups (ostracods and foraminifera) from the Sao Tomé-Principe archipelago in the Tropical East Atlantic and the Zanzibar archipelago in the western Indian Ocean. The manuscript is clear as to its methods and discussions, and its conclusions are of importance. I however see a few modifications that need to be made prior to publication, which may correspond to minor-moderate revisions. Among them, the most important regards references throughout the text, that are often problematic as they actually correspond to inadequate publications when compared to the topic specifically discussed. Throughout the text, it is surprising to see that the references cited are focused on recent ones, though ostracodologist got interested in these questions much earlier than 2017. In such a discussion, pioneer works by Witte or Jellinek should be cited within the main-text and not only relegated to the supplementary data. A second point is the use of abbreviations for studied stations in the two areas, the meaning of which is not explained anywhere (and appears to only be available in the supplementary data). This makes the results and discussion quite hard to follow.

Response: We appreciate the positive comments from the reviewer. We cited the older papers by Witte and Jellinek in relevant places throughout the manuscript. We also added other references as recommended by the reviewer. In section 2.2 about the sample processing method, we added one sentence explaining the sample number: "Sample ID is coded with site abbreviations plus collection number". In all following texts, we use the IDs to specify each sample in each site. We tend to think that the use of sample ID causes no ambiguity.

I am adding a number of comments below, as well as corrections in the attached pdf.

Figure 1: this figure is quite important to follow the text and it would be important to add somewhere the correspondence between the different sites studied in each of the two areas and the abbreviations used in all other figures/tables and throughout the text. The correspondence between the abbreviations and the stations is in the supplementary files but the remaining discussion is literally not understandable if this is not explained somewhere as we read a succession of abbreviations without understanding what they correspond to.

Response: We added the abbreviations of each site in the caption of Fig. 1 as suggested by the reviewer. However, we reckon that either the full names or abbreviations throughout the text serve the same function of denoting a sample. For example, when we say the MA samples in the fringing reef habitats have low diversity for foraminifera, the readers should refer to Fig. 4 which clearly shows the diversity of MA samples in the Unguja Island, Zanzibar. We then explained the low diversity as the result of medium algae coverage in transitional environments. Unless the readers are curious about the exact geographic position of the MA samples, they do not need to refer to Fig. 1. In such a case, spelling out MA as Mnemba Atoll does not help with understanding.

Lines 109-111: "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)".

"and references therein" should be added: this reference is a review, while there are tens and tens of works that have been published before and since, and could be cited here.

Response: We added another reference using microfossils for paleoenvironmental reconstruction. (Cronin, 1981).

Lines 141-143: "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."

In this presentation, it is not clear where "stable quartz sands and calcareous bioclastic sands" are found, are they like restricted to a specific area?

Response: the distribution of different types of substrates does not follow a clear geographic pattern. To avoid misunderstanding, we revised the sentence to be:

"In terms of substratum, a large proportion of the coastal area is covered by dark-colored volcanic sands and secondarily stable quartz sands and calcareous bioclastic sands."

Lines 145-159: in this paragraph, a number of references are inadequate. Narayan et al. (2022) is used as a reference for the position of the Zanzibar archipelago and its climatic characterization: this reference deals with the link between foraminifera and an appropriate reference should be found for the climate of the area. Similarly, Tian et al. (2024a) is used for the circulation system in the area, which should be replaced by an appropriate reference for this aspect.

Response: We replaced the references with (Mahongo and Shaghude, 2014) and (Painter, 2020).

General comment on the chapter "2.2 Sample processing and data integration"

A quite important number of published works have been used for the present analysis. I do understand that the space may be limited but the supplementary files should at least be mentioned here, indicating that all references and taxa are available there. It is currently available only in the legend of Table 2 but should be clearly written in the text as well.

Response: We added the following text at Line 190 in the main text:

"(Table 2; See Table S4 and supplementary data for the complete species occurrence list and literature cited)."

Lines 169-171: "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)".

This sentence raises two problems on my side. First, the reference Tian et al. (2024a), with regard to this specific matter, does not propose any specific discussion on how to count ostracods in a meaningful way, but rather refers to Yasuhara et al. (2017). Upon checking Yasuhara et al. (2017), there is also no reference to how ostracod specimens should be counted, or I may have totally missed it. On that question, the ostracodological literature provides more adapted references, for instance Boomer et al. (2003).

Response: We cited (Boomer et al., 2003) as suggested by the reviewer.

This first remark leads me to my second issue with this sentence lines 169 to 171. Let's say that we have 3 left valves, 3 right valves and 4 carapaces of species X from the exact same sample. If I understand well, then the counting would lead to 10 specimens in total for this example. But, the 3 right valves and the 3 left valves could well belong to only 3 individual that may have dissociated: counting them as 6 would lead to a bias in abundance evaluation.

Response: As stated in (Boomer et al., 2003), counting valves and carapaces each as one individual is the generally accepted practice in ostracod research. There are numerous studies following this standard methodology, including but not limited to (Tian et al., 2024; Yasuhara et al., 2017; Hong et al., 2022; Chiu et al., 2020; Yamaguchi et al., 2014; Hong et al., 2019). We thus followed the standard method. The case when one carapace disintegrates and preserves as two complete valves is likely but has not been quantitatively evaluated by considering the preservation bias and adult-juvenile ratio. In other words, all methods are potentially subject to different bias. Most importantly, most specimens in all our samples are found as single valves and carapaces take up less than 0.5% of total abundance no matter if it is counted as one or two. The counting methods do not contribute to any significant differences in our results.

Lines 180-188: it would be important to write "black on white" that biogeographic analysis is only performed for Sao-Tome area and why it is not performed for Zanzibar.

Response: This study primarily focuses on STP and the Zanzibar ostracod data is used for comparison to show heterogeneity of tropical shallow-marine ecosystems. We clearly stated that "To evaluate the biogeography of STP and more generally the TEA" at Line 187. The Zanzibar data has been published before, and its biogeography is beyond the scope of this study.

Figures 3, 4, 5: indicate in the legend what 0D, 1D, 2D, 1E, 2E mean.

Response: We revised the legend to be "Fig. 3. Species diversity (A) and evenness (B) of ostracod assemblages across Hill number orders *q*=0, *q*=1, and *q*=2".

Lines 308, 309: "Foraminifera diversity is generally high on fringing reefs, with one exception that the sand flat at ST2 is particularly diverse".

This sentence is unclear and should be rephrased.

Response: We rephrased it to be "Foraminifera diversity is generally high on fringing

reefs, but the sand flat site ST2 is also highly diverse.”

Beginning from line 309, abbreviations of stations are increasingly used. What they correspond to has not been detailed anywhere and the reader constantly needs to search through the figures to understand what is discussed exactly.

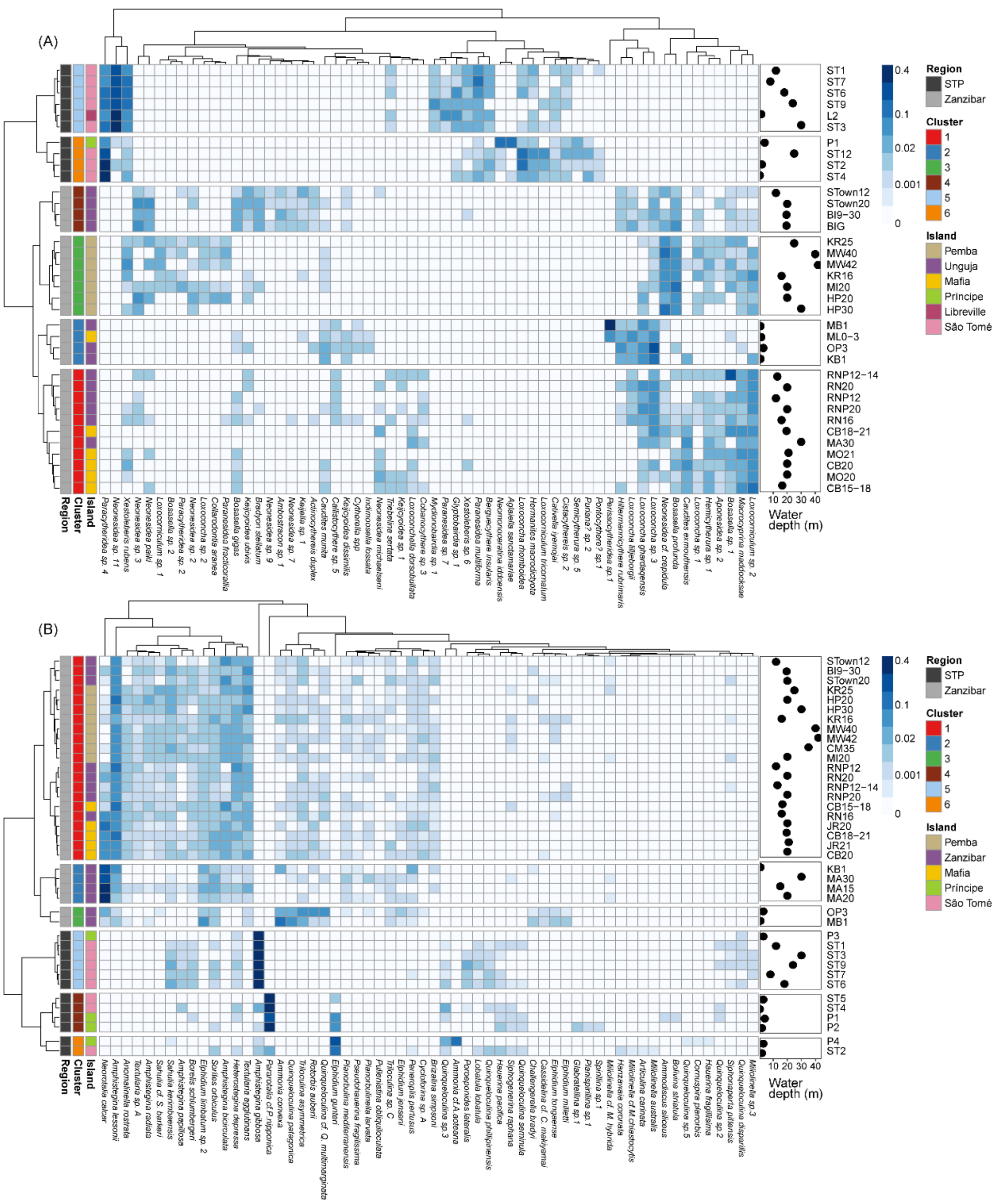
Response: Either the full names or abbreviations throughout the text serve the same function of denoting a sample. If the abbreviation tells us which sample it is, then we have fully conveyed our message.

Table 3: a number of things should be clarified in the legend, as (Intercept), s(Island), t value, Pr(>|t|), *, **.

Response: The intercept is the value of the dependent variable when all predictor variables in the model are equal to zero. s(Island) means the effect of island as a random variable. The t-value measures the size of the difference relative to the variation in the sample data. Pr(>|t|) represents the p-value associated with a specific predictor variable's t-statistic in a regression model. Asterisks show significant results ($p < 0.05$*, $p < 0.01$, $p < 0.001$***).**

Line 354 and following: the impact of human is evaluated but how was it evaluated? What does a “medium human impact” mean? Similarly in this paragraph, the mention to “intermediate water depths” is unclear, what does this mean? The same applies to “shallow samples”, “deep reefs”, “intermediate and deep waters”, “true reefs”? All in all, we need clarifications.

Response: We clearly stated in the Method section that “All variables were measured on site” at Line 228; “Algae coverage and human impact were handled as ordinal variables with three levels (i.e., low, medium, and high).” at Line 235. This means that we visually inspected every site during scuba diving to record the human impact as one ordinal variable of three levels. High human impacts are those sites where the benthic environments are severely damaged by human activities (e.g., overfishing). Low human impacts are the pristine sites not visited by local people. And in between we have medium level of human impact. We statistically evaluated how the diversity and composition of benthic assemblages vary across different levels of human impact. Our expression should have no ambiguity in the context. In terms of water depth, we stated in the Method section that our sampling sites cover a depth range of 0.5-30 m at Line 172. The words “shallow” and “deep” should have their literal meaning and intuitively tell the readers that a cluster includes mostly shallow or deep samples without a quantitative definition. To aid understanding, we added a side panel in Fig. 6 to show the water depth of each sample in each cluster. At Line 145, we specified that “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”. The words of “true reef” versus “marginal reef” are usually directly used in marine ecology studies without the need of clarification.



Lines 472-474: "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". This sentence is really hard to get. Could you rephrase and perhaps bring a bit more details? By "well-adapted ostracod composition", do you mean well-adapted ostracod taxa? Should references be added?

Response: We revised the sentence starting from Line 488 to be: "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 ostracod composition in terms of well-adapted dominant species."

As stated in the Method section at Line 208, Hill number at order q=2 measures the

number of dominant species by giving more weight to species relative abundance. This is the statistical definition of Hill number and thus does not need references.

Figure 8: there is a discrepancy between the text and the ecological categories mentioned for this figure.

Response: We made sure that the "reefal taxa", "phytal taxa", "bottom-dwelling taxa", and "brackish taxa" are consistently used throughout the manuscript.

Table 4: a number of things should be clarified in the legend, as SumOfSqs, F value, dist2land, Pr(>F), **, ***.

Response: SumOfSqs measures the variation explained by the model. F value is the ratio to compare whether the overall variances between multiple groups are significantly different. Pr(>F) is the p-value associated with the F-statistic. Asterisks show significant results ($p < 0.05$*, $p < 0.01$, $p < 0.001$***). Dist2land is replaced by 'distance to land'.**

Lines 601-603: "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)".

The reference is not adapted and should be replaced by one that really fits with the discussed aspect.

Response: We added another reference (Danielopol et al., 1994).

A number of similar comments are added directly in the pdf.

Boomer, I., Horne, D. J., and Slipper, I. J.: The use of ostracods in palaeoenvironmental studies, or what can you do with an ostracod shell?, The Paleontological Society Papers, 9, 153-180, 2003.
Chiu, W. T. R., Yasuhara, M., Cronin, T. M., Hunt, G., Gemery, L., and Wei, C. L.: Marine latitudinal diversity gradients, niche conservatism and out of the tropics and Arctic: Climatic sensitivity of small organisms, J. Biogeogr., 47, 817-828, https://doi.org/10.1111/jbi.13793, 2020.
Cronin, T. M.: Paleoclimatic implications of Late Pleistocene marine ostracodes from the St. Lawrence Lowlands, Micropaleontology, 27, 384–418, 1981.
Danielopol, D., Marmonier, P., Boulton, A., and Bonaduce, G.: World subterranean ostracod biogeography: dispersal or vicariance, Hydrobiologia, 287, 119-129, 1994.
Ford, B. M. and Roberts, J. D.: Latitudinal gradients of dispersal and niche processes mediating neutral assembly of marine fish communities, Mar. Biol., 165, 94, 2018.
Hong, Y., Yasuhara, M., Iwatani, H., and Mamo, B.: Baseline for ostracod-based northwestern Pacific and Indo-Pacific shallow-marine paleoenvironmental reconstructions: ecological modeling of species distributions, Biogeosciences, 16, 585-604, 2019.
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.
Mahongo, S. B. and Shaghude, Y. W.: Modelling the dynamics of the Tanzanian coastal waters, Journal of Oceanography and Marine Science, 5, 1-7, 2014.

Painter, S. C.: The biogeochemistry and oceanography of the East African Coastal Current, Prog. Oceanogr., 186, 102374, 2020.

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

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Yasuhara, M., Iwatani, H., Hunt, G., Okahashi, H., Kase, T., Hayashi, H., Irizuki, T., Aguilar, Y. M., Fernando, A. G. S., and Renema, W.: Cenozoic dynamics of shallow-marine biodiversity in the Western Pacific, J. Biogeogr., 44, 567-578, https://doi.org/10.1111/jbi.12880, 2017.