We thank the two anonymous reviewers for their valuable and critical reading of the manuscript, which were useful in improving the scientific quality and clarity of the work. A point-wise response is given below, with the original reviewer comments in italics, and our answers in blue and labelled as “Response”.

Kind regards,
Kirsty Edgar and co-authors

RESPONSE TO REVIEWER 1

General comments

The article presents a well-structured summary of our current knowledge of planktonic foraminiferal ecology and clearly points out current knowledge gaps. Perspectives for future research are highlighted in the abstract and the conclusions, but they remain rather vague in the article itself, so that both the abstract and the conclusions seem to be disconnected from the main body of the article. For example, eDNA and eRNA approaches are mentioned in the abstract and/or the conclusions, but not in the main article.

Similarly, it is repeatedly stated that observational and experimental data as well as modelling approaches are needed to improve our understanding of foraminiferal ecology, but the suggestions for future studies remain rather vague. What exactly should be done in future experimental/observational studies? How exactly can trait-based models help to understand foraminiferal ecology and fill current knowledge gaps? In my opinion, this aspect needs more focus and concrete examples if it is to be emphasized in the abstract and in the conclusions.

Response: Thanks for highlighting this discrepancy. We will revise the final section of the manuscript to provide more details on key aspects of each of the major traits for future experimental, observational and modelling research as well as where appropriate within the main text. For instance, in a new “*Suggestions for future research*” section that will replace the Conclusions section. An example of some new text is below for major traits with a focus on experimental/observational studies. Modelling contributions are discussed in response to a later comment.

“Planktic foraminifera are an ideal target group for testing trait-based approaches, as a relatively small number of functional traits can define their ecological niches in the modern ocean. However, many of the traits identified here remain poorly qualified and quantitatively constrained, requiring further observational and experimental laboratory-based work.

A key trait requiring further study is calcification. Its trade-offs (Table 2), particularly its hypothesised benefit of protection against grazing, are fundamental to current trait-based models for calcifying plankton but still lacks direct evidence (Barrett et al. 2025; Monteiro et al. 2016). We also require an understanding of the energetic costs of calcification and the mechanisms controlling biomineralization. This requires moving away from analogies largely based on physiological calcification studies of benthic foraminifera (e.g., De Nooijer et al 2009, De Nooijer et al 2014) to similar experiments on planktic foraminifera. At present, the poorly constrained relationship between calcification and seawater carbonate chemistry limits our ability to predict the impact of ocean acidification on foraminiferal growth and carbonate production. This knowledge gap also hampers the accurate modelling simulation of ocean alkalinity distribution and carbonate production in response to climate change.

Food availability can support metabolism to reduce the impacts of anthropogenic climate change on other physiological processes. Further understanding of foraminiferal predator-prey *dynamics is therefore urgently needed. For example, further culture and in-situ observations can improve our understanding of feeding, by providing quantitative data on (1) the role of bacteria, and (2) organic matter in foraminiferal diet - specifically protein acquisition from zooplankton versus phytoplankton, (3) prey-predator optimum length ratio, (4) prey encounter rates (successful and unsuccessful), and (5) average digestion and capture time of prey. These data could also (in part) be collected by analysing feeding vacuoles and metabarcoding analyses of samples.*

Photosymbiosis, a major trait among foraminifera, also requires further investigation. Culture and observational studies should focus on the impacts of environmental change on symbiosis. These include understanding what triggers change in symbiont hosting (e.g., bleaching, and hosting for symbiont-facultative species), which symbiont each species hosts, and the energy the symbiont provides its host.

Experiments that exploit the new breakthrough in multigenerational planktic foraminifera culturing will improve our knowledge of their life cycle, through understanding the traits and trade-offs associated with their development, e.g., metabolic rates, food uptake, reproduction, and importantly which species are capable of asexual reproduction and under what conditions this mode dominates. All of which will contribute to better data for improved modelling of planktic foraminifers.

Environmental DNA (eDNA) metabarcoding, which analyses the genetic material present in the environment, such as sediment, or water, is a powerful new tool for identifying and monitoring biodiversity, biogeography and reconstructing ecosystems and ecologies (Ruppert et al., 2019). This technique can also provide insights into community composition over timescales spanning several hundreds of thousands of years or longer, improving our understanding of the relationships between biodiversity, environment and climate (e.g., Ambrecht et al., 2019). However, the bulk of eDNA foraminiferal studies to date have focussed on benthic foraminifera. For instance, this technique has significantly increased the diversity of organic walled and "naked" foraminifera that are rarely observed, have few morphological characters for traditional species delimitation, and don't preserve well in the fossil record (Pawlowski et al., 2014). But eDNA holds great promise for investigating marine plankton, as it has the potential to overcome many of the data limitations that we currently face in this group with typically low standing stocks (de Vargas et al., 2015). It is a potentially more effective means of detecting species presence in an environment than observations alone (Malviya et al., 2016; Ser-Giacomi et al., 2018; Barrenechea Angeles et al., 2020) but can also contribute much more broadly. For instance, providing insights into plankton population size (Andres et al., 2023), response to environmental change (Cao et al., 2022) or predator-prey dynamics (Ruppert et al., 2019). A combination of molecular and microscopic approaches can also yield new insights, e.g., in benthic foraminifera it allowed rapid determination of multiple different feeding strategies driving diversity and abundance in several foraminiferal taxa (Schweizer et al., 2022), a question which is typically restricted to analysis of feeding vacuoles and laboratory experiments. However, further method development is still required as some groups are not as well represented by eDNA technique as others, e.g., specimens may visually be present in sediments not found in the eDNA analysis, likely because of limitations of the primer to detect certain groups (Barrenechea Angeles et al., 2020, Hoshino and Inagaki, 2024)

In general, there is a need to improve data reporting practices in the aforementioned studies by following guidance on data publishing (e.g. FAIR principles) and developing standardized, community agreed protocols for measuring traits to enhance our understanding of planktic foraminifera and how they are best modelled."

In addition, the article lacks a robust discussion of what challenges future studies may face when following the author's suggestions. Since this is a review and syntheses article, I do *not expect an extensive discussion. However, I think that the reader should at least be made aware of the major challenges associated with the suggested approaches. This is already partly done for observational and experimental studies, but modelling approaches are, in my opinion, presented much too idealized. For example, it is stated in the conclusions that models "can create theoretical frameworks akin to laboratory experiments". I think it is essential to mention that models are based on assumptions and simplifications, i.e., they will never be an exact replica of nature. The only model limitation discussed in the article is the lack of input data for foraminifera. But what does this imply for the reliability of model simulations? Under what conditions and to what extent can models be compared to real-life experiments and/or observations? Such thoughts should be included in the argumentation.*

Response: Agreed. In response to this comment, along with similar comments raised by Reviewer 2, we will add a new section to the manuscript discussing model limitations and challenges under a section called "*Suggestions for further research*" in addition to additional comments within the main text addressing minor comments that are detailed elsewhere in the reviews, e.g., L70-72 re. Gibbs et al. (2020) study. A taste of this is above. But we will also lay out some specific model assumptions, simplifications and challenges of current modelling and implications for outputs. *"However, whilst a powerful tool, numerical models are ultimately just that, models. They are by necessity based on assumptions and simplifications of the natural world. Model reliability and performance is highly dependent on the specific research question asked and the observations available against which models can be validated. For planktic foraminifera, the most abundant data for model calibration is sediment core top data and most foraminiferal models can reproduce the observed global biogeography of main species/ecogroups in sediment cores. However, less empirical data can be used for foraminiferal physiological model parameterisation. The growth rate and temperature dependency data from Lombard et al. (2009) are adopted by most plankton functional type models (e.g., PLAFOM, FORAMCLIM, PLANKTOM). However, less constraint exists for food preference and grazing efficiency, hampering us to simulate the observed low foraminiferal biomass. Trait-based models can dynamically calculate grazing rate based on body size (allometric law) and temperature/food availability. However, a recent study shows that planktic foraminifera have lower allometric scaling of energetic needs compared to other plankton when considered in the context of organic density and catchment volume (Burke et al. 2025). Therefore, key parameters needed to improve foraminiferal model performance include more quantitative data of fundamental parameters such as: growth rate, respiration rate, half-saturation constant, and grazing preferences."*

Finally, the language lacks clarity. Long sentences with punctuation problems and sometimes minor grammatical problems make it difficult to follow the argumentation of the article. However, this problem should be straightforward and easy to fix.

Response: Thank you for pointing this out. We will carefully review the article upon revision to improve clarity to ensure the argumentation is clear and easy to follow.

Specific comments

It may be helpful to specify some technical terms as not all readers may be experts in the field: L. 43: pseudopodial network; l. 45: pseudopodia; L. 95: cryptic species; Table 2: rhizopodial (rhizopodia is explained in l. 248; I would add the same short explanation to the table caption); L. 146: shell flux; L. 432: blue water

Response: Thanks for flagging this. We will describe all of these terms for the reader or use alternative phrases where there is an appropriate, clearer alternative.

L. 34: Do you mean fossil records among all phytoplankton groups"?

Response: Apologies for the lack of clarity. We intended to say that planktic foraminifera have one of the most comprehensive fossil records among ANY plankton group. We will amend the text to make this clearer.

L. 54-55: There is no clear link between these two paragraphs, which disrupts the flow of the text. Maybe you could add a connecting sentence to the paragraph beginning in l. 55.

Response: Thanks for highlighting this disconnect. We will tweak the text to make the connection clearer. For example, *"Developing a mechanistic understanding of the controls on planktic foraminifera diversity and distribution is essential to generating accurate predictions of how changing environmental conditions will impact planktic foraminifera communities and, ultimately, biogeochemical cycles (Dutkiewicz et al., 2020).*

An improved mechanistic understanding can contribute to trait-based approaches, which describe how species interact with each other and their environment based on measurable organismal characteristics or traits (e.g. size, resource acquisition mode and defence; Dutkiewicz et al., 2020)."

L. 70-72: I think it is important to state here how successful these trait-based models actually were in reproducing the sedimentary record, so that the reader can get an understanding of the current state of research. In the Gibbs et al. (2020) model, for example, the simulated evolutionary response progressed orders of magnitude too fast.

Response: Yes, we should have been clearer in acknowledging that models are not perfect solutions but rather valuable complementary tools. We will add an explicit reference to the challenges in the example highlighted, along with a broader discussion of the limitations and caveats associated with trait-based modelling. In the introduction "*While trait-based models have significant potential, they have inherent limitations. Like any models, they are a highly simplified version of natural systems. They may simplify complex ecological interactions and environmental influences, and the expression and importance of traits may vary by environment impacting generalisation. Additionally, trade-offs between traits are not always well understood or quantified, as for example, the absence or presence of symbionts in foraminifera. The eco-evolutionary model used by Gibbs et al. (2020), for instance, resulted in modelled trait evolution at rates orders of magnitude faster than observed in the fossil dataset, highlighting the need for caution when interpreting these model results. Despite these caveats, trait-based approaches present an exciting opportunity to leverage the exceptional fossil record of foraminifera to test our understanding of the modern range of environmental conditions and beyond, assess the universal applicability of traits and trade-offs through time and ultimately improve our understanding of evolutionary processes."*

We will also expand the limitations where needed in the main text and in a new section on Future Work at the end of the manuscript. See response to comments elsewhere for more.

L. 77: Since models are based on assumptions and simplifications, their results have to be interpreted with care. Therefore, I would not use the term 'vastly' here.

Response: Thank you for your suggestion. We will remove the word "vastly" here.

L. 78: The current formulation is quite misleading; do you mean the first modeling study on foraminifera?

Response: Apologies for the lack of clarity. While earlier models on planktic foraminifera exist (e.g., Žarić *et al*.,2006; Fraile *et al*., 2008, 2009; Lombard *et al*., 2011), these models are species-specific, characterising a limited number of taxa for which empirical data is available, and thus, cover a relatively narrow range of environmental conditions and groups. The Grigaroutou *et al*. (2019) study referred to in the text represents the first non-species-specific trait-based model. We will clarify this distinction in the revised text.

L. 97-99: This sentence seems to contradict itself. Do you mean "their presence in shallow marine seas"? If not, please elaborate on this further.

Response: We will clarify this sentence. Planktic foraminifera inhabit the pelagic zone (open ocean), which excludes shallow marine seas or coastal shelves. We will revise the text to make this point clearer.

Table 2: Why is an increased area to volume ratio beneficial? Is it due to the increased capture area? If yes, you should make clear that this is meant here. If not, you should explain this somewhere in the text.

Response: An increased area-to-volume ratio offered by spines probably provides multiple benefits, including increasing the prey capture area (as suggested), an important advantage in the low prey environments these taxa typically inhabit. In addition, increasing drag helps taxa to maintain buoyancy. These benefits are currently detailed in Section 2.1.2, but we will amend the table text to explicitly state "*increased prey capture area*", as positive buoyancy is already highlighted.

L. 138-139: This sentence seems to contradict itself. What do you mean by individuals reaching larger sizes in the tropics but smaller sizes in equatorial regions?

Response: Thanks for pointing this out. The term "equatorial regions" should indeed read "equatorial upwelling regions". We will amend the text accordingly.

L. 145: Do you mean "greater reproductive success"?

Response: Yes, we will make this clearer in the amended text.

L. 172-176: Why is an increased sinking rate beneficial? This seems to contradict Table 2, where negative buoyancy is listed as a cost, while positive buoyancy is listed as a benefit.

Response: Thank you for spotting this discrepancy. The text should read that spines lead to a *decrease* (not increase) in sinking rate, helping further to counterbalance the negative buoyancy created by the shell in these taxa. We will correct the text accordingly.

L. 205: "also" instead of "though"?

Response: Thanks for flagging this. We will amend the text to read "*However, many studies identify*" to better reflect that while some studies indicate a group-level response, others find a species-level response.

L. 212: What exactly do you mean by "resolving the aforementioned biological factors"? Could you elaborate on this further?

Response: This sentence refers to several key aspects, including resolving cryptic species, understanding regional plasticity, identifying what controls gametogenic calcite thickness, and determining the biomineralisation pathway. We will elaborate on these points in the revised text to improve clarity.

L. 217-220: This sentence is very long and difficult to read, maybe split it into two sentences?

Response: Thanks for flagging this. We will split this sentence in two to improve readability and review the rest of the manuscript to revise any other long sentences to increase overall clarity.

L. 219: Do you mean reduced calcification?

Response: Yes, we will amend the text to make this clear.

L. 261: Do you mean that foraminifera can capture prey items 2-3 times bigger than themselves while most zooplankton cannot? If yes, I would write "contrary to most zooplankton"

Response: Yes, this appears to be the case. The general predator-to-prey size ratio is about 10:1, although this varies across groups, e.g., ~ 1:1 for dinoflagellates, ~8:1 for ciliates or ~18:1 for copepods (Hansen *et al.*, 1994). However, foraminifera, particularly spinose taxa, stand out as one group capable of capturing prey items much larger than their shell size. We will make the suggested point.

L. 275-276: This sentence is difficult to understand. Maybe replace with something like "Under laboratory conditions, non-spinose species exhibit cannibalism, but whether they cannibalise in the natural habitat is unknown and considered unlikely due to very low foraminiferal abundance."

Response: Okay, we will rewrite this sentence as suggested.

L. 278-279: This sentence is difficult to understand. Do you mean "The temporal and spatial distribution of prey is a major cause of the regional distribution of foraminiferal species, which affects growth and fecundity via temperature."?

Response: Apologies for not being clearer. Sea surface temperature is often invoked as a dominant driver of planktonic foraminiferal diversity (and hence assemblage composition), abundance and body size (e.g., Morey et al., 2005; Rutherford et al., 1999 and Schmidt et al., 2004). However, food availability is also very important and may modify these temperature-based relationships. We will reword this sentence as suggested while clarifying that food availability acts "*in addition to temperature*" as a key influence.

L. 316-325: This paragraph seems to contradict the previous one in which it is stated that planktonic foraminifera do not undergo diapause. Could you elaborate more on the dormancy of Neogloboquadrina pachyderma and how it differs from those of benthic foraminifera and dinoflagellates mentioned in the previous paragraph?

Response: Thanks for flagging this inconsistency. We will amend this section to clarify that *N. pachyderma* is an exception among planktic foraminifera, with evidence suggesting it can survive inhospitable conditions via dormancy. We will further elaborate on how this form of dormancy differs from the diapause observed in benthic foraminifera and dinoflagellates, providing additional context where possible.

L. 348-358: The different variants of symbiosis described here are unknown to the reader when they read Table 1. Maybe it would be helpful to include a short definition of these terms in the table caption.

Response: Good suggestion. We will add this information to Table 1.

L. 381-382: What impact may it have on modeled foraminiferal ecology that we cannot simulate facultatively symbiont-bearing species?

Response: This is a good question, and we will address it in the revised text. We currently lack a mechanistic underpinning of facultative symbiosis validated by laboratory culture and observations to resolve the relative benefits of facultative symbiosis for the host, and the drivers of symbiosis in so-called facultative taxa. Hence, it is very difficult to model accurately. This is exemplified by a recent study developing the ForamECOGEniE model to simulate different symbiosis types (Ying *et al*., 2023), which was able to broadly replicate geographic and abundance patterns of spinose symbiont-bearing taxa and non-spinose, asymbiotic taxa but underestimated the abundance of the non-spinose symbiont-facultative group, particularly in the eastern equatorial Pacific. Intriguingly, if the abundance of the obligate and facultative symbiotic taxa are combined in the model, there is a good fit between the model and observations (see Figure 4 in Ying *et al.,* 2023). Hence, this may suggest that the groups exploit the same benefits from symbiosis and, at least for modelling purposes, may be approximated using the same symbiosis parameters.

L. 432-434: How does this sentence connect to the previous one?

Response: Thanks for pointing this out. We will amend this section to clarify that the sentence refers to a potential disadvantage of broadcast spawning and sexual reproduction - that any mismatches in the timing or location of reproduction can reduce the chances of successful fertilisation.

L. 451-453: I don't understand the part starting with "and ability". Maybe it would help to rewrite this part and put it into a new sentence.

Response: We will add a new sentence to this part to clarify that the ability to reproduce both sexually and asexually is an advantage for the group. Specifically, we will clarify that asexual reproduction is suggested to facilitate rapid population growth during the polar summer (e.g., Meilland et al., 2023). We will rework this section to present the advantages and disadvantages of both reproductive modes more clearly.

L. 457-459: You mention repeatedly that most traits are poorly constrained. What I am missing is a discussion of the actual potential and limitation of trait-based modeling in this regard. Which traits can be modeled, under which assumptions/simplifications can they be modeled, and which impact may that have on the informative value of the model results? I suggest discussion this briefly for each trait and giving a short summary in the conclusions.

Response: This is a good point. We will expand on this in the revision.

L. 478-483: I think that models are presented too idealized in this manuscript. It should at least be mentioned that models are based on assumptions and simplifications, which means that they are not equivalent to observations of real organisms.

Response: This is a good point. We will add sections in the introduction and within the manuscript to address model limitations. Please see response to comments earlier here and to Reviewer 2 for more.

Technical Corrections from L30-471

Response: We will make all the suggested technical corrections in the final manuscript.

References cited in response

Fraile, I. *et al.* Predicting the global distribution of planktonic foraminifera using a dynamic ecosystem model, *Biogeosciences*, 5, 891–911, https://doi.org/10.5194/bg-5-891-2008, 2008.

Fraile, I. *et al*. Modelling the seasonal distribution of planktonic foraminifera during the Last Glacial Maximum, *Paleogeography*, 24, PA2216, https://doi.org/10.1029/2008PA001686, 2009.

Gibbs, S. *et al*. Algal plankton turn to hunting to survive and recover from end-Cretaceous impact darkness. *Sci. Adv*. **6,** eabc9123.DOI:10.1126/sciadv.abc9123, 2020.

Hansen, B., Bjornsen P.K. & Hansen, P.J., The size ratio between planktonic predators and their prey, *Limnology and Oceanography*, 39, doi: 10.4319/lo.1994.39.2.0395, 1994.

Lombard, F. *et al*. Modelling the temperature dependent growth rates of planktic foraminifera, *Marine Micropaleontology*, 70, 1–7, https://doi.org/10.1016/j.marmicro.2008.09.004, 2009.

Lombard, F. *et al*. Modelling planktic foraminifer growth and distribution using an ecophysiological multi-species approach, *Biogeosciences*, 8, 853–873, https://doi.org/10.5194/bg-8-853-2011, 2011.

Meilland, J. *et al*. Rare but persistent asexual reproduction explains the success of planktonic foraminifera in polar oceans, *Journal of Plankton Research*, 45, 15–32, https://doi.org/10.1093/plankt/fbac069, 2023.

Morey, A.E., Mix, A.C, & Pisias, N.G. Planktonic foraminiferal assemblages preserved in surface sediments correspond to multiple environmental variables. *Quaternary Science Reviews*, 24, 925-950, 2005.

Rutherford, S., D'Hondt, S. & Prell, W. Environmental controls on the geographic distribution of zooplankton diversity. *Nature*, 400(6746), 749–753. https://doi.org/10.1038/23449, 1995.

Schmidt, D. N. *et al*. Size distribution of Holocene planktic foraminifer assemblages: Biogeography, ecology and adaptation. *Marine Micropaleontology*, 50(3–4), 319–338. https://doi.org/10.1016/S0377-8398(03)00098-7, 2004.

Ying, R. *et al*. ForamEcoGEnIE 2.0: incorporating symbiosis and spine traits into a trait-based global planktic foraminiferal model, *Geoscientific Model Development*, 16, 10.5194/gmd-16-813-2023, 2023.

Žarić, S., Schulz, M. & Mulitza, S. Global prediction of planktic foraminiferal fluxes from hydrographic and productivity data, *Biogeosciences*, 3, 187–207, https://doi.org/10.5194/bg-3-187-2006, 2006.