

We thank both reviewers for their constructive comments on the manuscript. We have made some major changes following the two reviewers' comments.

- Firstly, we changed the POC export unit conversion (Reviewer #1's 4th major comment) and slightly retuned the model to account for this change. This change generates better model-data comparison than the previous version.
- We also reformatted the text, improving the introduction and the model description as Reviewer #2 requested. The introduction now justifies the focus on the critical gap in foraminiferal model development and introduces better the traits of spine and symbiosis to the readers. The model description update now includes a new figure demonstrating the basic model structure.
- Lastly, we added additional discussions about why we need to increase the foraminifera complexity in a model and the possible limitations in the current parameterization.

These additions have increased the manuscript's length while improving its clarity. We hope the editor agrees with us that this was worthwhile.

We have responded to each comment below. Reviewer comments are shown in bold, our responses in blue and our actioned responses in red (with quoted text in italics).

## Responses to reviewer #2

### Major comments:

**1) While I agree on the importance of spines and symbiosis to better understand the role of foraminifera in plankton dynamics and key nutrient fluxes in the ocean, I found that the introduction was not strongly motivated to address this gap in knowledge. I think the introduction should be reformulated, stating primary questions and providing more feedback on why spines and symbiosis are important, and importantly, clearly describing the different functional types of foraminifera (instead of focusing on trait-based models; see next comment). In addition, I think the main application of this work goes beyond predicting foraminifer flux. If one wants only to predict nutrient fluxes, statistical models might do a good (and even better) job than mechanistic models. Clearly stating why mechanistic models are important would be helpful. In addition, I think the results should be revisited to provide more mechanistic explanation for the observed patterns: how the tradeoffs implemented here help to explain the model predictions?**

Thank you for highlighting the need for further detail. We were concerned about the length of the paper as well as the details needed and desired in a journal of this focus.

In response to the reviewer, we have reformatted the introduction to address the key modelling gap in the 2nd paragraph and gave an explicit description to symbiont/spine and their function in the 4th and 5th paragraph. The 2nd paragraph addresses the challenge of current foram models in the context of geological record analysis, i.e. not mechanistic and species-based. The 4th and 5th paragraphs now introduce the foraminifer spine/symbiosis and give clear definition of the 4 functional groups.

For the results part (i.e., mechanistic description), we added some more ecological explanations of how we determined the optimal parameter. This part was added in section 7.1.

**2) The authors put their model forward as a trait-based model. While I think that there is some room for interpretation for what a trait-based model is, I think the authors should be more careful (and specific) here. T.....However, it seems that foraminifera were assumed to have a fixed size in the model and only phytoplankton and zooplankton were assumed to have different size classes. Moreover, neither spines nor symbiosis is implemented using a trait-based approach in the strict sense. Therefore, I don't think the authors should rely too much of their motivation on trait-based modeling as their implementation of foraminifera ecology is mainly based on functional type modeling (and that is fine!).**

Currently most studies define the essence of trait-based models as using measurable functional traits rather than species to link ecosystem function directly. Generally, we agree with the reviewer that our model relies on the parameterisation rather than having several independent physiological processes. However, we argue that there is no fully trait-based ecosystem model in any coupled model. Darwin/EcoGENIE still uses plankton functional types because we lack the ability to map discrete functional types on a continuous spectrum such as body size. ForamEcoGENIE fixes the body size, but it does so as part of the size-based model as a unique "calcifying" zooplankton while zooplankton have a full size-

spectrum. While individual size will influence the growth rate and other parameters determined by allometric rules, we lack quantitative observations of developmental changes of growth rate, respiration etc to expand the model and include this approach.

We agree that the phrasing of trait-based model warrants more careful treatment and we have stated this more clearly this now in the model limitation part (Section 9).

**3) The model description requires a through revision as in its current form it is very hard to understand how the plankton ecosystem is being simulated (what are the tracers (i.e. Carbon, nitrogen, phosphorus..), what are the different plankton groups, how they interact, what are the mechanisms modelled and how these are implemented). A schematic could really help the reader here. Even if the model has been published elsewhere, many changes were made here and so a full description of the equations should be given (either in the main text or in the supplement. Please be careful with providing units and descriptions for all model abbreviations that appear in the text. It is also especially hard to follow the functional type modeling for foraminifera and how the new tradeoffs related to spines and symbiosis were implemented.**

We apologise for the unclear model description.

We have provided a new figure (Figure 1) to help demonstrate these four foraminifer types and ecosystem structure/tracers. We also now separate the model description section into 3 parts: cGENIE physics, EcoGenie plankton ecosystem framework, ForamEcoGENIE 1 contribution and ForamEcoGENIE 2 contribution.

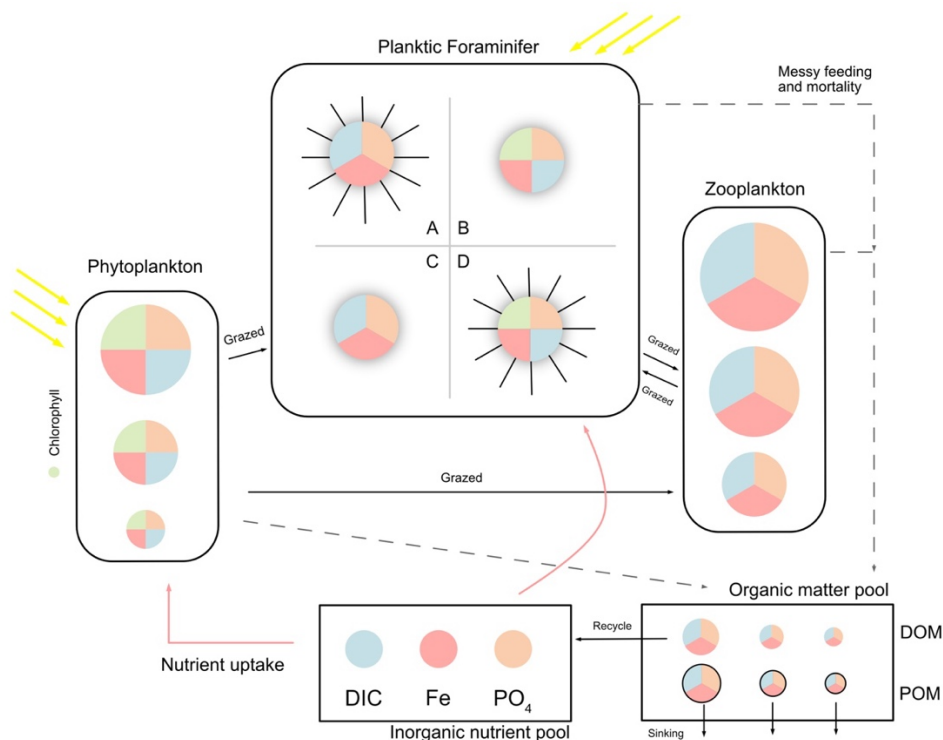


Figure 1. Schematic diagram of ForamEcoGENIE structure, showing the biogeochemical tracers (C, Fe, PO<sub>4</sub>) in different colours and plankton populations with various size classes. Physiological processes here include nutrient uptake (red arrows), organic matter production caused by messy feeding and mortality (dashed arrows), and zooplankton grazing (black arrows). A. symbiont-barren

spinose group; B. Symbiont-facultative non-spinose group; C. symbiont-barren non-spinose group. D. symbiont-obligate spinose group. DIC: dissolved inorganic carbon.

**4) I am not sure I agree with the way authors implement the spine and the symbiosis traits. The implementation of the “spine” trait is done so that spines incur an extra metabolic cost but offers a protection against grazing by decreasing the palatability of foraminifera and also allow them to be more efficient grazers. I am not entirely convinced by this approach for two reasons: i) how do authors calibrate the relative gain from lower palatability and the higher metabolic cost to build spines? A careful analysis to calibrate this tradeoff in a simple model would be very helpful and insightful. Was this provided previously in Foraminifera?; ii) spines widen the prey availability as explained in the manuscript. Since the authors are using a trait-based model with allometric relationships, why this was not mechanistically represented in the model? Instead, the authors simply decrease the half-saturation constant for grazing, which I don't think translates into the mechanism they are saying they want to model. Meanwhile, symbiosis is represented using the mixotrophy model by Ward and Follows (2016) so that foraminifera can both photosynthesize and consume prey but at a cost of not being as efficient as their specialized competitors. The model by Ward and Follows was developed mainly to describe constitutive mixotrophs, i.e. mixotrophs that possess their own photosystems but can also feed on planktonic prey. Symbiosis is a much more complex process that involves the host to maintain an entire population of their prey inside their cells. Do the authors think their simplified representation of mixotrophy is appropriate to represent symbiosis? What are the limitations of this approach? I suggest to critically consider these points and address throughout.**

1) We calibrated the spine trade-offs using Latin-hypercube sampling of the trade-off parameters to match observation. As for the exploration using a simple model, Grigoratou et al. (2019 Biogeosciences) and Grigoratou et al. (2021 Marine Micropaleontology) tested the trait trade off of calcification and spines. We have included a description of these prior exploratory studies in our last introduction/related method section.

2) It is a good point regarding model implementation and its current implementation of spine and symbiosis. But it is not feasible to generate a fully mechanistic model. Many physiological process descriptions (e.g., Photosynthesis rate-light intensity curve) are built on decades of experimental data, data which is missing for foraminifera. Specifically, we do not fully understand which environmental factors influence the development of spines, nor their full benefit, and their shape can differ between groups with a clear taxonomic but less clear functional difference.

As for symbiosis, foraminifer are not mixotroph as this is a symbiont host relationship. As the trade-offs and benefits of photosynthesis are not well understood, our approach was an approach to develop the skill in the absence of knowledge such as the energy flow between symbiont and host. By regarding foraminifer and symbiont as one entity, we can determine some of the benefits, such as survival in oligotroph areas which was impossible in the previous version. We base this combination on the knowledge that the symbionts will be digested by their host during reproduction (i.e., provide energy) and that they benefit growth (several papers by Allan Be).

We have addressed these model implementation limitations in the section 9.

**5) Before implementing the four different foraminifera types into a global model, it would have been very helpful to just analyze model behavior in a simpler model, a 0D model that consider idealized environmental conditions. The reader could then better understand how the tradeoffs related to spines and symbiosis play out.**

We focused on implementing the model in a 3-D framework because the basis for some of the model development have already been developed. As stated above, these tests have been performed by in Grigoratou et al. (2019 Biogeosciences) for calcification and Grigoratou et al. (2021 Marine Micropaleontology) for spines. The symbionts have similar implementation as Ward and Follows (2016, PNAS). A key constraint on a model with all four combined traits is the relative abundance across environmental gradients. The EcoGENIE model provides a consistent physical and biogeochemical framework to predict the spatial patterns in relative abundance along with predicted export production.

**6) The authors use an extensive dataset to compare their model predictions but I was surprised that the list of foraminifera sp used on this study and the respective functional type classification was not provided in the supplement.**

We added this table (Table S3) in the supplement.

**7) A strong point of this study is the number of observations that the authors could access to run their ensemble and compare their model predictions against. Although they can represent very well the relative abundance of most of the functional types at a global scale, the absolute biomass is not well predicted by the model. It is also hard to visualize model predictions against observations in Figures 5 and 6 but especially in Fig. 7 (not possible to see the observations in panel a) and in the seasonal plots (Figs. 9 and 10). Also, many of the observations in Figs 9 and 10 do not seem to align with the model. I acknowledge the challenge of comparing model predictions against observations, and that observations are also subjected to error, but I think authors must provide a better way to visualize seasonal patterns and acknowledge model limitations. Perhaps authors can start by comparing model predictions for total nutrients and total foraminifera biomass first since these tend to be easier to simulate than the biomass of different types? #**

We thank the reviewer's point on model-data comparison figures. The inconsistent model-data estimation of biomass/export has been largely solved, as referred to in the very first overview paragraph.

**Response to major comment 3 of the reviewer #1:** *"The low biomass to export production ratio shown in the manuscript it is likely caused by data processing. The modified model version which is calibrated against POC export with correct unit gives consistent magnitude for biomass and export now, though our main concern of underestimating these two metrics because of the limited temporal and spatial coverage in the data still remains. The true biomass is likely higher than observed (if all seasons were equally sampled) to match the high export production."*

As for the visualisation of biomass, export and seasonal patterns, we replotted the annual average map into two separate columns. Figure 7 is related to the outlier measurement method which is now removed in our revised manuscript (related comment copied below). We have also added a new map to describe the model seasonal peaks in biomass per foraminifera group (Fig 11, shown below), which have a generally good comparison with previous sediment trap study (Jonkers and Kučera, 2015, p.201).

*"To be clearer, using the median absolute deviation measurement can improve the model-data comparison as the data are sparse, and a few data points with high biomass/export variability will affect the overall scoring. Such high variability can be seasonal or caused by any other local changes to the environment such as storm events which is not resolved in the model. The new approach suggested by the reviewer of matching observation and model units means this is less of an issue; so we have removed this from the manuscript."*

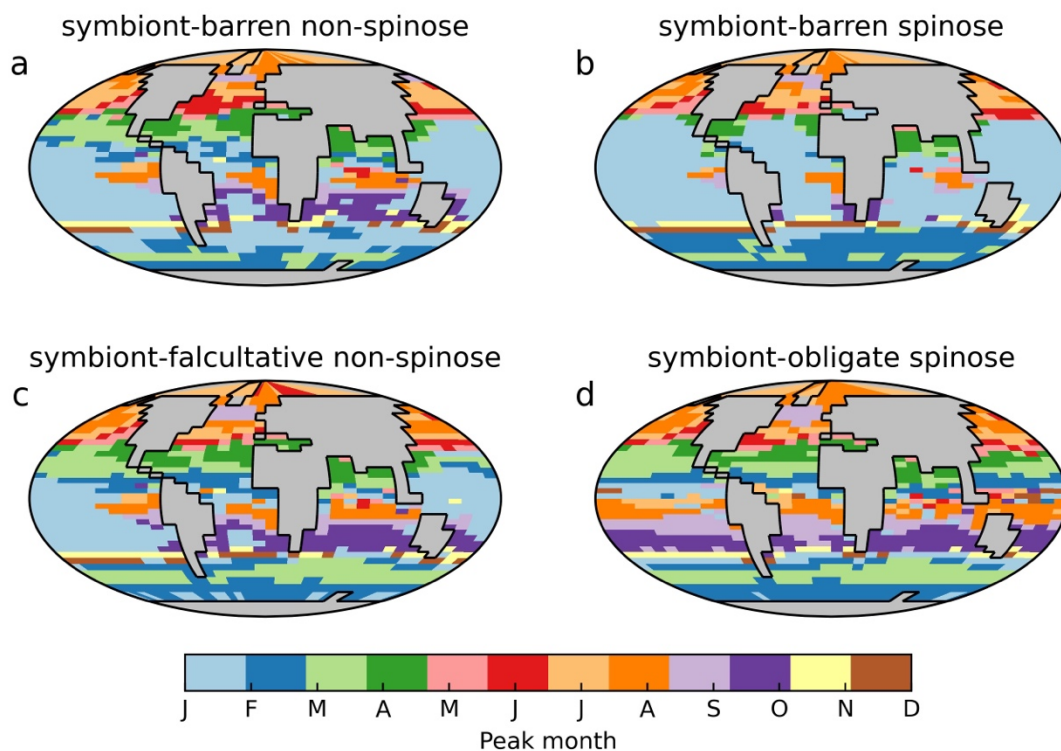


Figure 11. The peak month of modelled biomass annual time series of each foraminifer group.

#### Minor comments

- 1) Acronyms are used throughout the manuscript and in most of the cases with no previous description, please be sure to provide their definitions.

Acronyms are now defined in the first place of appearing.

**2) Model description: start with physics, then describe the biogeochemical tracers and then the plankton components.**

We reformatted the model description part and added the biogeochemical tracers in the 3.1 section now.

**3) The tradeoffs description requires a reformulation and more detail.**

We have given each trait and trade-off its own section .

**4) Section 2.4.1 is about respiration, but mortality and palatability are also described in there, confusing.**

We have changed the title to “calcification trade-offs” to be consistent with spine/symbiosis section.

**5) Line 245: Foraminifer predation cost: this description is weak, this is not a good way to frame this, for example, what if everyone is doing this but is doing it wrong?**

We do not understand the request of the reviewer here.

We have edited the predation cost part to help clarify any issues.

**6) Explain up front what the rain ratio means.**

We replaced the “rain ratio” term to  $P^{IC} \text{ to } POC \text{ ratio}$  so that it's clearer for readers.

**7) Perhaps table 2 could be reformulated to make it clear the differences between the different types, for example, I was surprised that the non-spinose has a Pp that is the same as the spinose type.**

We have reformatted this table and changed some font format, so it should be easier to read and compare.

**8) Table S1 and S2 should give list of sp and their functional classification.**

As major point 6. we have provided this in Table S3.

**9) Lines 380: I don't think comparing different models is that informative since they differ in their formulation and goal.**

This sentence is an introduction for readers of the general model performance. But we will not our readers that they are formulated in different ways and goals.

**10) If foram biomass is overestimated by 8 times, how off do you think the model predicts POC fluxes for each group? Can we still find these estimates robust?**

As major point 7, this has been revisited.

**11) I recommend to provide model code in a repository such as githb and perhaps zenodo.**

We provided model code and relevant data via zenodo as the journal required (readers can find in the **Code and data availability** section).



## References

Jonkers, L. and Kučera, M.: Global analysis of seasonality in the shell flux of extant planktonic Foraminifera, *Biogeosciences*, 12, 2207–2226, <https://doi.org/10.5194/bg-12-2207-2015>, 2015.

Grigoratou, M., Monteiro, F. M., Schmidt, D. N., Wilson, J. D., Ward, B. A., and Ridgwell, A.: A trait-based modelling approach to planktonic foraminifera ecology, *Biogeosciences*, 16, 1469–1492, <https://doi.org/10/gj349g>, 2019.

Grigoratou, M., Monteiro, F. M., Ridgwell, A., and Schmidt, D. N.: Investigating the benefits and costs of spines and diet on planktonic foraminifera distribution with a trait-based ecosystem model, *Marine Micropaleontology*, 102004, <https://doi.org/10/gkbn65>, 2021.

Ward, B. A. and Follows, M. J.: Marine mixotrophy increases trophic transfer efficiency, mean organism size, and vertical carbon flux, *Proc Natl Acad Sci USA*, 113, 2958–2963, <https://doi.org/10/ggnmm5>, 2016.