

First we would like to say thank to the reviewer for taking the time to comment on our study (the **reviewers** comments are marked in **black** below, the **authors** comments in **red**). We identified a few of the reviewers main concerns and summarise our responses below:

- 1) A major concern was that some of the facts were not correct, which lead to misleading outcomes. While writing this paper, we were referring to an earlier discussion version of the Buitenhuis et al., (2013) study which incorrectly showed foraminiferal abundance to be more than 4 orders of magnitude higher than in reality. After correcting this fact, we have revised the motivations and implications of this study.
- 2) The reviewer also expressed concern about the theoretical basis of the model. We emphasise that the model design goes beyond simply incorporating laboratory based temperature ranges to determine the foraminiferal distributions. Growth rates in the model are the result of the antagonism between food inputs (nutrition, photosynthesis) and the physiological expenses of the organisms (respiration). And each of these physiological processes varies with one of more of the forcing variables: temperature, food and light. Since it is currently impossible, based on the available knowledge, to incorporate the influence of all ecological and physiological processes on foraminiferal abundance, the second component of the model uses multinet plankton tow data to calibrate the empirical relationships between growth rates and abundance model, effectively allowing us to bridge this sizeable knowledge gap. The parameters of this calibration integrate the influence of the processes unresolved by the model. For a full appreciation of the model design, interested readers are encouraged to refer to the model description in Lombard et al., 2011.
- 3) Somewhat related to the above point: several reoccurring concerns of the reviewer are related to i) the impact of changes in food and temperature can't be disentangled and ii) a future projection is a sensitivity test, rather than reality. We completely agree that future projections are sensitivity studies and that it is not directly possible to separate the impact of temperature and food on foraminiferal distributions in nature. This is precisely why we turn to a model to attempt to explore the potential relative impacts of projected changes in food, temperature and light on future foraminiferal distributions. We turn to a model when don't have the data to answer a question we are interested in pursuing. When relevant data becomes available we will be in a good position to re-evaluate the model design and performance.

I have read with great interest the manuscript of Tilla Roy and co-authors on 'Projected impacts of climate change and ocean acidification on the global biogeography of planktonic foraminifera'. Modelling the various effects of environmental change on the production of foraminifers from empirical data help to better understand past, present, and future scenarios of ocean and climate change. In turn, considering the limited base of data used here (only 8 out of some 50 morphotypes, and possibly many more genotypes), modelling approaches as the one presented here are mere sensitivity studies, and any further interpretation should be done with care. Unfortunately, the manuscript is based on some facts, which are not correct, and the final outcome of some lines of thought is incoherent and misleading. Nonetheless, I would assume that the manuscript will make a nice asset to the current understanding of planktic foraminifers and ocean acidification when getting the basic assumptions right, and when carefully interpreting and discussing some of the model results.

We acknowledge that a climate change projection is by its very nature a sensitivity study. It was not our intention to overstate the results, but just to describe the results of our simulations, to summarise many of the caveats and suggest how our confidence in the model projections could be improved.

We have listed many caveats related to the model results in the section on Modelling Foraminifera: strengths and limitations. Perhaps they did not feature prominently enough in the paper because they are somewhat 'hidden' in the Methods section. To increase the visibility of the caveats, we have moved this section to the Introduction.

Similarly, the Model performance section that includes suggestions on how our confidence in the model projections could be improved was also hidden in the Methods sections. Part of this section has now been moved to the discussion (this was suggested by Reviewer 2).

As we detail below, some of the basic assumptions were based on an error in an online discussion paper. These assumptions have been corrected in light of the final published paper.

Starting from the abstract, it is very unlikely that planktic foraminifer calcite production will significantly affect marine carbon cycle (Buitenhuis et al., 2013, *Earth Syst. Sci. Data*, 5, 227–239).

Unfortunately, at the time of writing this paper, we were referring to an earlier discussion version of the Buitenhuis et al., 2013 paper that showed that the concentration of planktic foraminiferal biomass is 42.7 $\mu\text{g C IL}^{-1}$: the highest amount of any of the PFTs presented in the study. This number reduced by more than 4 orders in magnitude to 0.03 in the final version of the paper. Some of the motivations and implications of this paper were based on this incorrect number. In light of the correct number, the misleading introductory statements and conclusions have been removed from the paper.

In addition, production of the calcareous planktic foraminifer tests has close to zero effect on the short-term marine CO₂ budget by releasing the same amount of CO₂ to the ambient seawater as fixed by test calcite.

We did not intend to infer that foraminifera are a major control on atmospheric CO₂, nevertheless under present conditions about 0.6 mol of CO₂ are released per mole of calcium carbonate produced. This is still a significant amount given the magnitude of carbonate production by planktonic foraminifera. This ratio will increase with rising anthropogenic CO₂ due to the decrease in the buffer capacity of seawater. Changes in the net abundance of foraminifera should produce a small feedback on atmospheric CO₂ concentrations. We have removed some of the introductory statements on the carbonate-CO₂ feedbacks, since in this study we are not interested in overemphasising this point.

Highlighted for the first time in the abstract, it is stated that geographical shifts [in planktic foraminifer species distribution] are driven by other factors (i.e. temperature (T) only) than vertical shifts (i.e., 'multiple drivers', again T and phytoplankton [possibly as prey]). To me, it is not clear why vertical and horizontal effects should result from different causes.

Essentially, the reason we can get different vertical and horizontal effects is because food, light and temperature can have impacts on foraminiferal abundances that can be uncorrelated and either act to reinforce or counteract each other's impact on foraminiferal abundances. Also, the drivers themselves may not be well correlated. Under climate change, Earth system models simulate increases in ocean temperature in most regions, yet PP can either decrease or increase. Furthermore, the food requirements of each species represented in the model is unique representing different strategies that foraminifera use to feed and grow. Symbiotic species have a strong dependence on light availability. Therefore they mostly display horizontal effects and vertical shifts that are restricted to the euphotic zone (upper 200 m). Species that don't rely on symbionts have display horizontal and unrestricted vertical responses because they don't rely directly on light. They can travel as deep as the food source. Species that require more concentrated food sources are more likely to respond to changes in the distribution of prey and they may do so despite the temperature being less favourable. This complexity is taken into account in the ORCA/PISCES/FORAMCLIM models and leads to a wide range of horizontal and vertical responses that we have summarized in this study. For example, take *N. pachyderma*, the dominant species in the high-latitudes, which drives much of the change in the simulated total foraminiferal abundance. It's abundance is reduced throughout most of it's habitat range in response to a warming ocean, but abundance increases over patches of the ocean, and shifts to depth in some regions, mirroring food availability. By contrast, for *G. sacculifer* and *G. ruber* and shift polewards and deeper in the water column both as the thermocline and nutricline deepen, yet food

availability does not contribute to the latitudinal shifts because the column-integrated food availability is not altered significantly throughout the habitat range.

Since, we did not necessarily want the reader to focus on vertical and horizontal effects being caused by different drivers, rather on that multiple drivers drive the future change in foraminiferal biogeography, we have altered the way we present these results in the abstract:

“Temperature is the dominant control on the future change in the biogeography of foraminifera. Yet food availability can either act to reinforce or counteract the temperature driven changes. In the tropics/subtropics the largely-temperature driven shift to depth is enhanced by the increased concentration of phytoplankton at depth shift of the food. In the higher latitudes the food-driven response partly offsets the temperature-driven reduction both in the subsurface and across large regions, particularly around the Antarctic continent. “

In addition, it is almost impossible to disentangle the effects of temperature and phytoplankton distribution, the distribution of the latter being largely driven by temperature (plus nutrient concentration [also related to T at the global scale], and light).

We know that disentangling both effects is complicated, and could not be easily achieved by means other than a model. And, it is precisely for this reason that it becomes interesting to use a model to investigate how the stressors (food, temperature or light) could contribute to the future changes in the distributions of these organisms.

Further, planktic foraminifer species occur over a very broad range of temperature, and are not good indicators of absolute T and changes in T, as indicated by figure 1 (from Lombard et al., 2009, Marine Micropaleontology;

Although we apply this broad temperature tolerance in the model, we do not claim that foraminifera are good indicators of absolute temperature. Using the relationships in Figure 1, we do assume that abundance increases progressively towards the optimum temperature and sharply drops at the high-extreme end of the range. And more importantly the model incorporates i) the response to multiple environmental drivers (food, temperature and light) and ii) the impact of these drivers on independent process (photosynthesis, nutrition and respiration). The purpose of the study is to project how the multiple drivers could influence the future biogeography of foraminifera, through simulating their potential growth rates and abundances. To appreciate the above complexity readers must refer to the detailed model description in Lombard et al (2011). A detailed model description was purposefully excluded from this paper.

and not correctly reproduced here;

The growth rates shown are correct, but they are just showing the temperature component of the nutrition rate see the component (i.e. $\exp(-T)/1 + \exp(-T) + \exp(-T)$) from Equation 1 in Lombard et al., (2011), not the full response. To avoid confusion, we also include the contributions of temperature on photosynthesis and respiration to better reproduce the growth rates shown in Lombard et al., (2009).

plus wrong reference – Limnology and Oceanography), and correctly stated later in the manuscript.

Reference has been corrected

The limits of planktic foraminifer ‘optimum temperature’ (Lombard et al. 2009, fig. 2) are identical with the limits of global ocean SST (just above 30°C in the Indian Ocean, and WPWP), and hydrographic fronts (polar fronts, ~3-4°C). Ecological changes across hydrographic fronts include more than changes in T only, and effects on planktic foraminifera are again- not easy to disentangle.

We understand the reviewers concern, however we must remind the reviewer how the temperature is included in the model: it is more than just putting a limit on the optimal temperature range. As explained earlier, other drivers (which we agree are important when considering changes in foraminifera growth potential and abundance across hydrographic fronts) are also included (light, food availability). Other potentially important drivers, such as salinity, have not been incorporated in the model, because of the paucity of ecophysiological data on the growth response to this variable. However, since the effect of changing light penetration in water column and food availability are taken into account, the potential impact of these variables on foraminiferal distributions across hydrographic fronts should be resolved in the models, given that the gradients in temperature, food and light across hydrographic fronts themselves are well represented in the model.

To my impression, growth rate curves produced by Lombard et al. (2009 and 2011) from laboratory data, can't be directly be applied to natural systems, and would result in over-interpretation. For example, specimens dwelling in warm, stratified, and oligotrophic waters of the subtropical gyres would possibly not reproduce at a monthly cycle due to lack of food, and might continue to grow. Assuming a monthly reproduction cycle, growth rates would be assumed to high in this case.

We acknowledge that physiological laboratory experiments are artificial, yet they are currently the most direct approach available for quantifying the growth response of foraminifera to specific environmental changes.

However we should point out that the growth rate curves in Lombard et al., 2009 and 2011 are just one component of the model. The model has been calibrated against multinet plankton tow data from a wide range of ocean environments, including the tropical Pacific, which is one of the most oligotrophic places (Field, 2004; Kuroyanagi and Kawahata, 2004; Schiebel et al., 2001, 2004; Watkins et al., 1996; 1998). The model has also been validated against abundance data from both the surface ocean and sediment core tops and gave quite good agreement between simulated and observed abundance. With a better quantitative understanding of the relationship between abundance and foraminiferal reproduction and other poorly understood aspects of foraminiferal biology, future model development could lead to an improved representation of abundance.

In addition to the more general comments above, I have listed some more specific remarks in the following.

- 1) What, to the author's idea, is the difference between 'environmental' and 'ecological' change (p. 10085, line 15).

Good point. "Climatic" would be better than "environmental" since environmental includes "ecological". Environmental has been replaced by "Climatic".

In the same paragraph, references for all of the seven points would strengthen the given statements.

Done

...need to include two references...

- 2) P. 10086, lines 15-19: Planktic foraminifers are not dominant plankton in the oceans as can be seen from the final version of the paper of Buitenhuis et al. (2013), and planktic foraminifers are minor contributors to ballasting (please please have a second look at the reference given (De La Rocha & Passow, 2007).

As detailed above, the implications on the carbon cycle referred to here, were based on the older and incorrect version of the Buitenhuis et al., 2013 paper in which there was a large overestimate of the contribution of foraminifera to the standing stock of planktonic biomass. In light of the revised final Buitenhuis 2013 study, I have revised my introductory statements and now no longer refer to foraminifera as a dominant planktonic group.

3) P. 10087, lines 7-10: Bijma et al. (1990) show limits in T and S, and Bijma et al (1992) show that other factors than T are also important to explain distribution pattern. In general, many references are not correctly used. Another example: Beer et al. (2010) show that carbonate ion concentration exerts different effects on the test production of different species, and not 'generally reduced' calcification as stated by the authors in lines 377-378.

The sentence has been adjusted to "Temperature exerts a first order control on the distribution of foraminifera (Rutherford *et al.*, 1999). Each species has a unique optimum temperature range with a fairly sharp drop in their growth rates at either extreme (Figure S1). Yet other factors have been shown to influence the distribution patterns of foraminifera (e.g. Bijma *et al.*, 1990; Bijma *et al.*, 1992). Light also plays an important role...."

The sentence referencing Beer et al. (2010) now reads: "calcification by foraminifera is sensitive to carbonate ion concentrations." To account for the differing signs of the responses.

4) P. 10087, lines 15-18: The fact that symbiont bearing species are dominant in oligotrophic gyres does not say that those species are most frequent in oligotrophic gyres. On the contrary, also symbiont bearing species are more frequent at higher than at lower levels of prey.

Correction has been made. The phrase "so occur most frequently in the oligotrophic gyres" has been replaced by "so dominate the abundance in the oligotrophic gyres."

5) P. 10087, line 26: 'microfossil sediments' do possibly not exist. Please change to 'microfossil rich sediments'.

Done

6) P. 10088, line 22: '. . . historical emissions. . .' of what? Please specify.

Done. Added "historical (1860–1999) CO₂ emissions (Marland and Andres, 2005)"

7) P. 10092, line 16: Riebesell et al. (2000) discuss coccolithophorids, and I can not see any connection to the present manuscript.

Originally both Riebesell et al. (2000) and Iglesias-Rodriguez et al., (2008) were included to make an analogy to coccolithophores: foraminifera may also show variability in their response to carbonate concentrations between strains. The Riebesell et al. (2000) has been removed and replaced with "Langer, G, Nehrke, G, Probert, I, Ly, J, and Ziveri, P. (2009) Strain-specific responses of *Emiliana huxleyi* to changing seawater carbonate chemistry. *Biogeosciences*, **6**, 2637–2646.", as it better summarises these intra-specific variations.

8) P. 10092, line 26-28: Please have a look at Schiebel and Movellan (2012), and the information on size-related biomass of planktic foraminifers.

An example of the impact of the size variation based on the size spectrum in Schiebel and Movellan (2012) has now been included:

"A convincing explanation for the weak relationship between biomass and abundance could be related to the FORAMCLIM model not resolving variations in shell size: a wide range of abundances can be fitted the same total biomass of a foraminiferal population depending on how this biomass is distributed over different size classes. To illustrate this point, we can take the typical biomass size spectrum from Schiebel and Mollevan (2012): a 1 m³ of water with a foraminiferal abundance with 100 individuals m⁻³ is grouped into 3 size classes 100–150 μm, 150–250 μm, and 250+ μm with each size class having 75, 19 and 6 individuals respectively. A small change in the size spectrum (e.g. having just two more individuals in the largest and intermediate size classes, i.e. 75, 21, 8 individuals in each size class) would require a large decrease in the total abundance from N_T=100 to N_T=68 individuals to match the same total biomass"

10) P. 10093, lines 15-18: What happens at tropical, temperate, and subpolar waters, which you have (possibly) not included in your model?

We do not 'include' the regions in the model: the global distribution patterns simulated by the model emerge based on the combination of the local environmental conditions and the physiological requirements of each foraminifer species. The sentence referred to here simply describes the broadscale pattern of species of dominance. The description has been expanded to "... with *G. bulloides* in the more productive upwelling areas and temperate zones, *G. ruber* in the subtropical gyres, *N. pachyderma* in the subpolar/polar regions and *G. sacculifer* dominating in the tropical/subtropical regions in between".

11) P. 10095, line 5-12: I agree that CPR data are interesting. CPR data are resolved for different water depth, nor integrating all of the surface water layers. In addition, CPR data only include the >200 µm size fraction, and hence miss most of the planktic foraminifer fauna.

We have elaborated on the other limitations of CPR data in the paper as suggested by the reviewer: " Another potential complication with foraminiferal CPR data is that the sample may not represent the mean surface ocean distribution of foraminifera because i) the CPR does not resolve different water depths, and ii) the large mesh size (>200 µm) means that much of the foraminiferal fauna is not captured in the samples. Nevertheless, by taking the statistics of the CPR sampling protocol into account, it should be possible to use the total abundance of foraminifera recorded in the original written records for each CPR sample to evaluate the simulated changes in total foraminiferal abundance from the model."

12) P. 10095, line 20 and following: Please specify what you mean by climate change, i.e. the absolute change in T, CO₂, etc.

Done. Sentenced changed to "Under climate change temperature, food availability and light were perturbed such that the total foraminiferal abundance...". Note that we do not model the influence of CO₂ on foraminiferal abundance.

13) P. 10096, lines 9-18: Looking at three species only does not really give a good idea of what will really happen, and you might want to choose your wording more carefully.

This paper is a modeling study projecting the impacts of climate change on planktonic foraminifera, so in the results section it is appropriate to simply present what happens in the simulations. To emphasise (and remind the reader) that we are referring to the simulation results we have added "In the simulation, three species dominated the changes in total foraminiferal abundance: the two abundant warm-water species."

14) P. 10097, line 13: 'too warm'

Done

15) Chapter 3.4: You may want to consider the paper of Feely et al. (2004)

Done

16) P. 10100, line 10: I like the idea of 'wild foraminifera'. However, 'in nature' might be the better wording.

Done

17) De Villiers 2004, and Barker and Elderfield (2002) discuss data from sediment samples, and which include other effects (e.g., early diagenesis), on foraminifer tests than in the water column. Same in p. 10103, line 12-15: In sediments, a range of entirely different processes are to be considered, which can possibly not be discussed in the manuscript.

The reference to De Villiers has been removed. Barker and Elderfield has been left in, since we do specify 'coretops' when citing this reference. It is interesting still to state that the responses recorded in coretops differ from those recorded in laboratory experiments and in the field, especially since all 3 sources of data are frequently cited in the same papers (Beer

et al., 2010), ALderidge et al., 2012). But as suggested by the reviewer, we do not elaborate on the processes controlling the calcification responses recorded in the sediment top cores.

18) P. 10100, line 26: Phosphate concentration does possibly not affect heterotrophic planktic foraminifers.

True, since no evidence exists that phosphate actively reduces carbonate production (only through studies of spatial correlations between nutrient concentrations and size-normalised weights) phosphate has been removed.

19) P. 10101, line 23: The morpho-species *G. siphonifera* includes at least two species (Huber et al. 1997, Darling et al. 1997, De Vargas et al. 2002)

Yes, but here we are just talking about the simulated responses and we only include one *G. siphonifera* species in the model. We acknowledge the potential complication associated with not resolving cryptic species in the model later in the section, i.e. "...Another important factor that will influence how diversity responds to climate change is that most foraminiferal morphospecies have many genotypes that exhibit specific ecology, habitat preferences and biogeography (Aurahs *et al.*, 2009)..."

20) From p. 10101, line 27 to p. 10102, line 12: Can you present any proof for your statements?

In the model simulations we do show proof that temperature and food availability influence projected foraminifera distributions. Unfortunately, little observational evidence exists on the impact of anthropogenic change on planktonic foraminifera. We elaborate in more detail on the present evidence for historical change in foram distributions and the need for more observational data in the final section of the paper.

21) P. 10103, lines 20-21: How might symbiont bearing species react, which can possibly not decide to move to the deeper water column?

We do simulate the response of symbiont bearing species in response to climate change in the model. Most of the simulated tropical/subtropical response of total foraminiferal abundance to climate change is dominated by the symbiont bearing foraminifera *G. ruber* and *G. sacculifer*. In the tropics, the abundance of both of these species shifts deeper in the water column, predominantly in response to temperature and food availability. The presence of symbionts restricts the vertical shifts of to the euphotic zone (up to 200 m). Although less light is available for photosynthesis by the algal symbionts when foraminifera move deeper in the water column: in the model the loss due to reduced light availability is compensated by the increased growth due to the improved conditions (temperature and food availability) deeper in the water column in the future.

In reality the response of symbiont-bearing foraminifera to light is likely to be much more complex than simulated in the model. For example, the colour of the symbionts and the excess photosynthesis produced (which results in the secretion of dissolved sugars) may help to attract potential prey using these visual and chemical signals (typical of algal aggregates and copepods alike). If such behaviour is important then foraminifera could conceivably stay in upper part of the euphotic zone, despite improvements in the growth conditions (temperature and food availability) in the deeper part of the euphotic zone. Yet we currently know too little about such processes to include them in the model.