

## REVIEWER1

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.

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 CO<sub>2</sub> budget by releasing the same amount of CO<sub>2</sub> to the ambient seawater as fixed by test calcite.

We did not intend to infer that foraminifera are a major control on atmospheric CO<sub>2</sub>, nevertheless under present conditions about 0.6 mol of CO<sub>2</sub> 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 CO<sub>2</sub> due to the decrease in the buffer capacity of seawater. Changes in the net abundance of foraminifera should produce a small feedback on atmospheric CO<sub>2</sub> concentrations. We have removed some of the introductory statements on the carbonate-CO<sub>2</sub> 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. Its abundance is reduced throughout most of its habitat range in response to a warming ocean, but abundance increases over patches of the ocean, and shifts to depth in some regions, responding to increases in 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.

We have now included part of the above paragraph in the discussion on climate impacts. Also, 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 ability 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 foraminifers 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.  $\exp(\dots)/(1+\exp(\dots)+\exp(\dots))$ ) 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 foraminifers 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

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 m<sup>3</sup> of water with a foraminiferal abundance with 100 individuals m<sup>-3</sup> 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<sub>T</sub>=100 to N<sub>T</sub>=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, CO<sub>2</sub>, 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 CO<sub>2</sub> 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.

## REVIEWER2

We would like to thank the reviewer for working through our manuscript thoroughly. First we briefly summarise by commenting on some of the reviewers most significant concerns:

1) The reviewer identified some incorrect comments in the manuscript, such as the large impact of the marine carbon cycle. These comments largely reflected that we referred to an earlier online discussion version of the Buitenhuis et al., (2013) which erroneously showed foraminiferal standing stocks to be of more than four orders of magnitude larger than in reality. The results are unaffected, yet the motivations and implications of our results have been corrected to adjust for the much lower standing stocks of foraminifera in the global ocean.

2) The reviewer requested that we get some indication of how much of the total abundance the 8 species in the FORAMCLIM represent. This was a nice suggestion that helps put our results into perspective. We now show, based on the MARGO database of sediment top core data, that the eight species represented in FORAMCLIM account for about 50% of the total foraminiferal abundance. Thus, even though we represent only about 20% of the species diversity we capture a large proportion of the total abundance because the model includes the key dominant species. The projected changes in the foraminiferal abundance simulated here, would therefore be expected to have a significant impact on total abundance.

3) Both reviewers asked for a clearer explanation about the uncertainty in abundance due to not including variation in foraminiferal size in the model. We have included a detailed example to clarify this point.



4) A question about the uncertainty in the projected responses was raised by the reviewer. Unfortunately with only a single model it isn't feasible to determine the uncertainty in the future projection. Ideally this would require a multimodel study and a model-data evaluation of the interannual variability in of foraminiferal growth/abundance in response to environmental change. We could then compare the magnitudes of the future change in foraminiferal abundance to comparable present-day responses. In a dedicated section of the paper we emphasise the need for a database of the present-day changes in foraminifer abundance with concomitant environmental variables, so that it will be possible to carry out such a study.

The manuscript "Projected impacts of climate change and ocean acidification on the global biogeography of planktonic foraminifera" by Tilla Roy et al. describes the effect of climate change, including ocean acidification (OA) on the distribution of the most abundant planktonic foraminiferal species. This is based on models results from an Earth system model incorporating temperature, food availability (plankton biomass) and light as the main drivers of foraminiferal biogeography. Results indicate shifts in foraminiferal abundance and diversity, depending on the region and or species to sometimes huge extents.

The research is original and provides interesting data to the community. The model setup is state of the art and data from the literature was incorporated appropriately. The presented data seems to be of appropriate quality. In a few cases the discussion of the data in relation to the already existing literature needs to be extended to give a fuller and more correct view, as indicated below. Also some of the statements and conclusions drawn are not correct. I strongly encourage the authors to carefully check the grammar and language, preferably by a professional. I would recommend publication of this manuscript after major revisions have been carried out. I wish the authors good luck with the revisions and remain available for further feedback and discussions.

Comments: General: - manuscript could be shortened in some cases to make it more concise. Figure captions starting with "The". rephrase, e.g. Fig.6:"Zonally averaged changes...."

Done

-wrong tense: e.g. l.279 under climate change .... shifts... polewards, in this case it should be rather "was shifted". This is the case in many more examples, I would highly recommend to consult a language editor -the adjective of foraminifera is foraminiferal not foraminifer (e.g. caption of

Fig.1)

The results section has been changed to past tense and the adjectives of foraminifera have been corrected.

-narrative order is sometimes confusing, eg. l. 88 -90 distinguishes spinose and nonspinose forams, however, the term spinose has been used earlier without introducing the term (l. 82). BGD has a broad audience, therefore explaining such terms is crucial (same goes for explaining OA, see comments below)

Done

-some figures have stripes (eg 3a, b, 4a,c,d,5a,5c), please remove

This shouldn't be an issue with the figure quality and should just require turning of the anti- aliasing option on the software used to view postscript figures. In any case, we will ensure that there are no issues with the final submitted figures.

-The abstract mentions: "changes in the marine carbon cycle would be expected...", however, this has not been discussed, also the potential effect remains questionable.

In the discussion version of the Buitenhuis et al. 2013 (the version referred to in writing this paper), the standing stock was quoted to be at least 4 orders of magnitude higher than in final Buitenhuis et al., 2013 paper. Based on the final published paper of Buitenhuis et al., 2013, rather than the earlier online discussion paper, the paper has been modified (i.e. foraminifera are now only a small contributor to the standing stock of planktonic biomass and therefore changes in their abundance not be expected to have a strong impact on the organic particulate carbon flux). Yet, changes in the marine carbonate flux would be expected and this has been discussed.

Comments according to sections: Introduction: l.48: of past what? word missing.

Done

l.52: add citation

The book chapter Honjo et al., 1996 has been added which summarises studies on the biogenic calcium carbonate flux.

I.63: explain what OA is and why reduction in carbonate production would decrease atmospheric CO<sub>2</sub> (broad audience of BGD).

We have included a more detailed description of Ocean acidification and carbonate production. We have deemphasised the CO<sub>2</sub> feedbacks, because it was never our intention for this effect to be the key motivation of the paper.

I.66: not depends but results from

Done

I.71: rephrase sentence "Towards this end, in this study investigate present and future changes in the 3D distribution..." (?)

Done

I.86: impact on, not of

Done

I. 93: to reconstruct

Done

I. 111:"," should be after the bracket

Done

I.117: change . with , after concentration

Done

I.127: living not live

Done

I.127: add citations

Citation included to the FORAMCLIM description

I.128: growth rate or growth? what is the unit of the growthrate? (um/ ug per day?)

It is in units of d<sup>-1</sup>, but to avoid confusion we now refer instead to the increase in weight per day  $\Delta W$ , ( $\int \text{gC d}^{-1}$ ). More details in Lombard et al.,

2011.

I.139 what are the factors a and b?

The scaling factors of the calibration between growth rates and abundance (See Lombard et al., (2011) for details).

Table 1: %P really in percent or as fraction?? eg. should 0.46 not really be 46%? (caption says percentage),

It is a fraction. To avoid confusion, we adopt the same symbol (i.e. %P) for this constant as used in the original reference describing the FORAMCLIM model (Lombard et al., 2011).

is  $S_{nb}$  based on 250 ug or 250um individual (caption vs text I. 148)? references for the values?

It is based on 250 um individual. The error in the Table caption has been corrected.

I. 160/ 161: I understand that the number of foraminiferal species incorporated in the model needs to be limited, however, it would be interesting to see how high the discrepancy is between only using 8 species and the reality? A short comment on this, e.g. differentiated into the main regions of the model (tropics/ subtropics, etc and surface/ whole watercolumn) would be highly appreciated. (Maybe this can be achieved by comparison to MARGO database?)

This is an interesting point and something we had actually been interested in looking into. Based on the global compilation of topcore sediment data (Kucera et al., 2004), we now show that the 8 species represented in the FORAMCLIM model account for about 50% of the total foraminiferal abundance. This fact provides a much clearer perspective on our results. For example in the discussion section we now explain "... in the tropics/subtropics the 40% decrease in total simulated foraminiferal abundance could produce a 20% reduction in total planktic foraminiferal carbonate production, given that the 8 species in the FORAMCLIM model account for about 50% of the 'true' total planktonic foraminiferal abundance (Kucera *et al.*, 2004)."

I.166: sampling

Done

I.171: "and calculate..." rephrase

Done

l.171: explain Omega C here (l. 342 is too late in the document)

Done

1. 182: replace the with that

Sentence has been split into two parts and rewritten.

l. 188: replace [] with ()

Done

l.189: et al.

Done

l. 202/ 203: it has been possible to reproduce foraminifera in the lab (benthic ones), see for instance **Toyofuku et al., 2008**, G3, 9, 5, Q05005, doi:10.1029/2007GC001772 and **deNooijer et al., 2009**, Biogeosciences, 6, 2669–2675, 2009

The adjective “planktonic” to clarify that, here, we are referring only to planktonic foraminifera, not to all foraminifera.

l. 203: the fact that planktics do not reproduce in the lab might not be the only fact allowing us to conclude that foraminifera behave differently in the lab. Lab experiments are always artificial and do never correspond to real live, however, it is all we have to manipulate certain parameters.

We agree completely. A new sentence has been added to stress this point: “It is important to keep in mind that although all physiological laboratory experiments are artificial, they are currently the most direct approach available for quantifying the growth response of foraminifera to specific environmental changes.”

l. 210/211: please explain a bit more.

Given the interest in this statement (both reviewers ask the authors to explain this point in more detail), we include the following explanation: “... a wide range of abundances can be fitted to 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 m<sup>3</sup> of water

with a foraminiferal abundance with 100 individuals  $m^{-3}$  is grouped into 3 size classes 100–150  $\mu m$ , 150–250  $\mu m$ , and 250+  $\mu m$  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 100 to 68 individuals to match the same total biomass.”

I. 233: define RMSE

Done

I. 232-235: I think other numbers need to be cited here (those of the present study only), e.g. abundance: the one of the here presented data is 3-24 based on the table, in I. 233 "3-25%" is mentioned, I assume 25 is from the Fraile study, same for RMSE

Done. That is, only those of the present study are cited.

I.245 maybe put at different spot in manuscript, maybe more as a discussion, conclusion section, not as method?

Done. This section has been removed to the discussion.

I.245 five not 5

Done

Results: fig.4 add timeframe to "future change" (eg year 2100)

Done

I. 283: the total abundance IS shifted to greater depths...

Done

I.284: reference to Fig5a is not correct here

Done

I.286: under climate change scenario: rephrase

Done

Fig 4 could benefit if Fig. 4a and c were also showing the future scenarios, not only present day.

Such a figure would be somewhat redundant. The purpose of this figure is to give an indication of the magnitude of the present magnitudes and future change in the surface abundance and diversity, particularly given that many observations are made at the ocean surface.

I.286: are the decreases in the tropics and increase in subpolar regions statistically significant? What are the estimated errors of the simulation & calculation of the Shannon diversity index?

Since this is sensitivity study based on a single Earth system model, there is no way to determine an error in the uncertainty of the projection. To estimate uncertainties in climate projections it is necessary to perform a multi-model study (e.g. Bopp et al., 2013). Nevertheless, the Earth system model output used to drive the FORAMCLIM model has been extensively evaluated over the historical period (Schneider et al., 2008).

Schneider, B., Bopp, L., Gehlen, M., Segschneider, J., Frolicher, T. L., Cadule, P., ... & Joos, F. (2008). Climate-induced interannual variability of marine primary and export production in three global coupled climate carbon cycle models.

We now reference this study in the IPSL model description section when we mention that this model has been evaluated of the historical period.

Figure 6: While Abund And Rabund are correctly defined in both the materials section and the caption of Figure 6, it is not used elsewhere (not even in the respective axis labeling of Figure 6) and should therefore be omitted to avoid confusion.

Done

Fig. 6: what exactly refers to surface?

The surface ocean box has a thickness of 10 m and this information has now been included in the IPSL model description.

I.301: verb is missing after N. dutertrei (decrease?)

The missing verb has been added

I.304: "was accompanied by small increases"-> judging from Fig, 6c the decrease of 20% in N.pac is matched by the total increase of 20% in G.bull, N.inc, N.dut , therefore I would not say that generally species diversity is low, but that it seems that in the futures species diversity seems to



increase in the higher lats (shift from N.pac to G.bull, N.inc, N.dut), also seen in fig. 5d.

This section has been reworded. The main point was to emphasise that the only significant change in abundance in the high-latitudes is the decrease in N. pachyderma (the abundance of G.bull, N.inc, N.dut barely change) and this indirectly drives an increase in the relative abundance of the other species present.

I.310: Both, Change order: Figure 8 before Figure 7, also change order in results section

Done

I.320: "changes in nutrition rates" ? Please explain this, as I do not see how temperature would affect nutrition rate solely in such a way that abundance shift. I would more attribute this to the physiological optimum temperature for a give species.

There is strong interplay between temperature and all physiological foraminiferal processes. It is true that in reality it is not possible to have temperature solely impacting the nutrition rates, i.e. respiration, photosynthesis and all other physiological processes will also be impacted. This is why we use the model. The impacts of temperature on nutrition, photosynthesis and respiration are built into the FORAMCLIM model, which allows us to disentangle the response of each physiological process to temperature (or food and light), such as the impact of temperature on nutrition.

We introduce this fact in the beginning of this section.

From a biological point of view, the effect of temperature on foraminiferal nutrition is complex. It impacts behaviour (plankton can retract their cytoplasm and refuse to feed), enzymology (digestive enzymes are only functional within a certain temperature range, yet their efficiency varies within this range), and cytology (membranes can be more fluid with increasing temperature, yet only functional under a given range that is controlled by the composition of the phospholipids). Each of these processes has a unique optimum temperature range and can impact the growth and abundance of a foraminiferal species.

Fig. 8: Please quickly comment about the general patterns of change in temperature and food observed, e.g. why is phytoplankton concentration in

the Southern Ocean increasing in the future?

A consistent result in future projections is that phytoplankton concentration in the Southern Ocean increase both where mixed layer depths shoal and also around the poles where there is a reduction in sea ice extent. Both of these processes can alleviate light limitation on phytoplankton growth. The concentration of iron also plays a central role, since PP can only increase in the presence of iron (see Steinacher et al., 2010 for an explanation of the response of PP in the simulation used in this study, and also for a complete discussion of a range of PP responses in other Earth system models forced with the same IPCC SRES AR2 emission scenario).

Steinacher, M., Joos, F., Frölicher, T. L., Bopp, L., Cadule, P., Cocco, V., ... & Segschneider, J. (2010). Projected 21st century decrease in marine productivity: a multi-model analysis. *Biogeosciences*, 7(3), 979-1005.

We now include the following sentence in this section of the results: “The increase in phytoplankton abundance in the Southern Ocean is a reoccurring response in future climate change simulations and partly result from the alleviation of light and/or temperature limitation (Steinacher et al., 2010).”

We also point readers to this study and another multimodel study of Roy et al., 2011 in the IPSL model description section: “The IPSL model simulations .... have contributed to multimodel studies of the future change in marine primary productivity (Steinacher et al., 2010) and the carbon cycle (Roy et al., 2011).”

Fig.9: Why is the increase in habitat for *O.uni*, *G.sacc*, *G.Siph* and *Grub* not reflected in a relative increase in abundance? The negative impact of a decrease in habitat seems to be well reflected in a decrease in foraminiferal abundance, but not vice versa. This should be discussed in more detail in lines 417-421, as I find this interesting and puzzling. As stated in l. 415 it is generally expected that pelagic species should have the potential to escape to more favourable conditions, however, this study shows that while the more favourable conditions are predicted, abundance still drop (or do at least not benefit as much as would be expected).

The habitat area is the region where the conditions are sufficient for growth of a foraminifer given the ambient light, food and temperature conditions. It does not equate to the conditions being equally favourable. Under climate change a greater volume of the ocean may be within the temperature

range that a particular species can exist, but this new habitat can be suboptimal. Take *G. ruber* and *G. sacculifer* for example. The available habitat of these species increases as it shifts towards the subtropical region in response to changes in temperature and deeper in the water column. Yet, large parts of the subtropical ocean contain oligotrophic gyres where food resources are scarce.

Fig. 11: red contours hardly visible (exp. Fig11a). change colour scheme so to avoid reddish colours in the figure to enhance contrast

The color of the contours has been changed for improved visibility.

Fig. 11c) make clear in caption this is for the future, not present. In general the captions are sometimes too short. The more information is found in the figures, the better.

Done

I.355 add citation

This is a result from this present study, so can't have a citation. The section has been reworded to make clarify this.

Discussion: order should reflect that of results. rearrange (e. OA is last in results and first in discussion) the addition of subheadings could increase readability

The order of the discussion has been changed to reflect the order of the results.

I.367: "which reduces foraminiferAL calcification rates"

Done

I.367 this statement is not correct in its current form, it is different for different species and also different studies have found different responses, see e.g. Keul et al . 2013 (Biogeosciences, 10, 6185–6198, 2013, [www.biogeosciences.net/10/6185/2013/](http://www.biogeosciences.net/10/6185/2013/) doi:10.5194/bg-10-6185-2013) for an overview.

Although this statement may be true for the species in this study, it is true that some species do not respond to ocean acidification in the same way: the sentence has been modified and the Keul et al., (2013) reference inserted. "Such population–driven impacts on carbonate production could

be further amplified or dampened if calcification rates themselves are impacted by anthropogenic change. Ocean acidification and the associated decrease in carbonate concentrations can alter foraminiferal calcification rates (Lombard *et al.* 2010; Keul *et al.*, 2013), while higher ocean temperatures could accelerate calcification rates within certain temperature windows”

I. 368: can accelerate: only to a certain degree in a certain temperature window

The sentence has been reworded.

I.371: add reference to respective figure

Done

I.376: "are a response to higher atmospheric CO<sub>2</sub> concentrations" this statement in this general form is not true. On a physiological level, this might not be true for at least a few foraminifera, see for instance the study in Keul *et al.* 2013 where the disentanglement in the different C-system parameters allowed the conclusion that not the increase in CO<sub>2</sub> but the reduction in CO<sub>3</sub><sup>2-</sup> causes the observed decrease in shell weights.

We agree that it is more likely that the decrease in carbonate ion concentration drives the shell thinning and not the increase in atmospheric CO<sub>2</sub>. The former is a consequence of the latter. We now state that shell thinning could be attributed to both the decrease in the carbonate ion concentration and the increase in atmospheric CO<sub>2</sub> and have referenced Keul *et al.*, 2013.

I.377: "is generally reduced at low carbonate ion concentrations" This is not true for all foraminifera (e.g. *C. gaudichaudii* in Hikami *et al.* 2011, see the discussion and references in Keul *et al.* 2013)

Although we did use the word ‘generally’ here, which implies that this is not universally true for all species, we have modified this sentence to “sensitive to change in carbonate ion concentrations”

I.382: how is this assessed to be 20%? ...

We apply the quantitative relationships between carbonate ion concentrations and shell weights from the laboratory studies to the

distributions simulated in the FORAMCLIM model. We do not dwell too heavily on this statement because this is a gross extrapolation and neglects many of the other processes known to control calcification rates, such as temperature. We now include a more detailed reference to the laboratory studies and species used to make this rough potential estimate of the carbonate-only impact on calcification.

I.385: omit are

Done

I.386: and are thusly... (or better: consequently)

Done

I.387:  $\Omega = 1$  is the theoretical threshold, however, studies have found that foraminifera can thrive in waters with  $\Omega < 1$ , or can be also affected by waters  $> 1$ . This fact should at least be shortly mentioned.

We have not been able to locate a study documenting planktonic foraminifera that thrive at saturation states less than 1 and planktonic foraminifera live in the upper water column of the pelagic ocean where such levels are unlikely under present day conditions. Perhaps the reviewer is referring to studies of benthic foraminifera, which are not the subject of this paper?

I.397: "magnitude and the sign of the slope"... this strongly contrast the earlier statement in I. 377 "calcification is generally reduced at lower carbonate concentration"....! (the statement in I. 377 is not correct, see earlier comments)

The statement in I377 has been corrected (see correction associated with I377 above).

I.398: it does not only depend on how relationships were assessed, e.g. in laboratory cultures on the same species fundamental differences in the calcification response have been found (see eg. the discussion in Keul et al. 2013 on the differing calcification responses of *Marginopora* to OA in culture)

To take into account the intra-species variation in calcification responses the sentence has been modified to "...Both the magnitude and the sign of the slope of the relationships between shell weight and carbonate ion concentrations vary between and within a species (Keul *et al.*, 2013)..."

I. 416: add citation to Figure 9 (as a general comment, the discussion would be easier to navigate if comments such as 'we show' are backed up by the specific Figure references, also I. 422 ref. to fig. 6)

Done

I.437: each species' preferred..

Done

I.467: how would such a shift to deeper waters affect photosynthesis of symbionts and consequently foraminiferal growth?

We do get a lower photosynthesis for the foraminifera living deeper in the water column relative to the individuals living shallower in the water column, but the net effect of this downward shift is masked by the overall increase in photosynthesis with the increase in ocean temperatures with climate change. Also, the lower contribution of photosynthesis to growth deeper in the water column is compensated for by the higher contribution of nutrition to growth due to the improved temperature conditions and increased food supply.

Figures 9 and 10 seem a bit blurry

Since the original submission, these figures have been replaced for the upload to BGD.

References:

Titles are capitalized in some

Capitalized titles have been corrected.

I. 643: odd paragraph

Done

I.603: delete space after P in Pole

Done

I.592 and I.526: "pp Page": check I.579 and 523: issue and or page numbers seem to be missing

Done

l.514: 275-&: check

Done

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# **Projected impacts of climate change and ocean acidification on the global biogeography of planktonic foraminifera**

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1 **Abstract**

2 Planktonic foraminifera are a major contributor to the deep carbonate-flux and their microfossil  
3 deposits form one of the richest databases for reconstructing paleoenvironments, particularly through  
4 changes in their taxonomic and shell composition. Using an empirically-based planktonic foraminifer  
5 model that incorporates three known major physiological drivers of their biogeography—temperature,  
6 food and light—we investigate i) the global redistribution of planktonic foraminifera under  
7 anthropogenic climate change, and ii) the alteration of the carbonate chemistry of foraminiferal habitat  
8 with ocean acidification. The present-day and future (2090–2100) 3D distributions of foraminifera are  
9 simulated using temperature, plankton biomass, and light from an Earth system model forced with  
10 historical and a future (IPCC A2) high CO<sub>2</sub> emission scenario. Foraminiferal abundance and diversity  
11 are projected to decrease in the tropics and subpolar regions and increase in the subtropics and  
12 around the poles. Temperature is the dominant control on the future change in the biogeography of  
13 foraminifera. Yet food availability acts to either reinforce or counteract the temperature driven  
14 changes. In the tropics/subtropics the largely temperature driven shift to depth is enhanced by the  
15 increased concentration of phytoplankton at depth. In the higher latitudes the food-driven response  
16 partly offsets the temperature-driven reduction both in the subsurface and across large geographical  
17 regions. The large-scale rearrangements in foraminiferal abundance, and the reduction of the  
18 carbonate ion concentrations of the habitat range of planktonic foraminifers—from 10–30 μmol kg<sup>-1</sup> in  
19 their polar/subpolar habitats to 30–70 μmol kg<sup>-1</sup> in their subtropical/tropical habitats— would be  
20 expected to lead to changes in the marine carbonate flux. High-latitude species are most vulnerable  
21 to anthropogenic change: their abundance and available habitat decrease and up to 10% of the  
22 volume of their habitat drops below the calcite saturation horizon.

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**Deleted:** In the tropics, the geographical shifts are driven by temperature, while the vertical shifts are driven by both temperature and food availability. In the high-latitudes, vertical shifts are driven by food availability, while geographical shifts are driven by both food availability and temperature
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## 52 1. Introduction

53 Large-scale changes to the biogeography and shell chemistry of planktonic foraminifera have the  
 54 potential to alter the marine carbonate flux as planktonic foraminifera form shells of calcium carbonate  
 55 (tests). Through the sinking of their tests to the seafloor, planktonic foraminifera contribute as much  
 56 as 32–80% to the global flux of calcium carbonate (Schiebel, 2002), despite their relatively sparse  
 57 distribution throughout the ocean (Buitenhuis *et al.*, 2013). Thus, they represent one of the three  
 58 planktonic groups that dominate the oceanic carbonate flux alongside coccolithophores and  
 59 pteropods (Honjo, 1996). Indeed, much of the seafloor is covered by foraminiferal tests. This is partly  
 60 due to the efficient transport of foraminifera to the ocean floor since they are comparatively large  
 61 (mostly between 0.01 to 1 mm) and have rapid sinking speeds (Berger & Piper, 1972). Also, the tests  
 62 of foraminifera are relatively well preserved because they are composed of calcite: the less soluble of  
 63 the biogenic forms of calcium carbonate.

64 Under future scenarios of climate change, ocean acidification is projected to reduce the carbonate  
 65 production by planktonic calcifiers (Orr *et al.*, 2005). As the ocean absorbs excess atmospheric CO<sub>2</sub>,  
 66 the increase in dissolved CO<sub>2</sub> results in a reduction in pH (i.e. an increase in acidity) and a reduction  
 67 in the concentration of carbonate ions [CO<sub>3</sub><sup>2-</sup>]. This decrease in carbonate concentration makes it  
 68 more difficult for calcifying organisms to form biogenic calcium carbonate. It also leads to a reduction  
 69 in the calcium carbonate saturation state (Ω<sub>c</sub>) of the oceans (Feely *et al.*, 2004), where

70 
$$\Omega_c = \frac{[Ca^{2+}][CO_3^{2-}]}{K_{sp}^{CaCO_2}}$$
[Ca<sup>2+</sup>] and [CO<sub>3</sub><sup>2-</sup>] are the calcium and carbonate ion concentrations and K<sub>sp</sub>

71 is the stoichiometric solubility product of calcite (CaCO<sub>3</sub>).

72 Present-day responses of planktonic foraminifera to anthropogenic change should provide a 'living  
 73 laboratory' for interpreting past responses to climatic change that have been recorded in the  
 74 sediments over geological timescales. Foraminifera are expected to be useful biological indicators of  
 75 anthropogenic climate change in the marine environment because:

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where 
$$\Omega_c = \frac{[Ca^{2+}][CO_3^{2-}]}{K_{sp}^{CaCO_2}}$$
 [Ca<sup>2+</sup>]

and [CO<sub>3</sub><sup>2-</sup>] are the calcium and carbonate ion concentrations and K<sub>sp</sub> is the ... [1]

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- 125 • foraminifera are established proxies of past climatic conditions (Kucera *et al.*, 2005) and, by  
126 corollary, should 'record' future climate change,
- 127 • the present-day global distribution of foraminifera is one of the most well known of all oceanic  
128 taxa (Rutherford *et al.*, 1999), and can provide a useful baseline for measuring change,
- 129 • there are no known specific predators of foraminifera (Hemleben *et al.*, 1989), so, changes in  
130 the distributions of foraminifera are more likely to reflect climatic rather than ecological  
131 changes,
- 132 • the spatial distributions of pelagic organisms are expected to shift faster in response to  
133 climate change than demersal species (Pereira *et al.*, 2010),
- 134 • the growth rates and abundances of foraminifera are very responsive to changes in  
135 temperature, particularly at the limit of their temperature range (Rutherford *et al.*, 1999),
- 136 • historical changes in foraminiferal abundance have been shown to reflect anthropogenic  
137 climate change (Field *et al.*, 2006), and
- 138 • changes in the abundance and distribution of foraminifera are well preserved in ocean  
139 sediments, and can be measured from plankton tows and sediment traps.

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140 Temperature, food availability and light traits demarcate much of the foraminiferal distribution  
141 throughout the global ocean (Hemleben *et al.*, 1989). Temperature exerts a first order control on the  
142 distribution of foraminifera (Rutherford *et al.*, 1999). Each species has a unique optimum temperature  
143 range with a fairly sharp drop in their growth rates at either extreme (Lombard *et al.*, 2009a; Figure  
144 S1). Yet other factors have been shown to influence the distribution patterns of foraminifera (e.g.  
145 Fairbanks *et al.*, 1982; Bijma *et al.*, 1990; Bijma *et al.*, 1992). Light also plays an important role in the  
146 distribution of many foraminifera species, both directly through providing energy to the algal  
147 symbionts hosted by some species of foraminifera (Spero & Lea, 1993), and indirectly by controlling  
148 the distribution of the foraminiferal prey (Bijma *et al.*, 1992). There are some generalizations that can  
149 be made about the broadscale biogeography of foraminifera based on light availability. Planktonic  
150 foraminifera can be divided into to two groups based on whether or not their tests carry spines

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154 | (spinose) or not (non-spinose). Many of the spinose species host algal symbionts that can contribute  
155 | to the growth of the foraminifera. Species with algal symbionts are generally optimized for shallow,  
156 | high-light, low-nutrient environments, so dominate the abundance in the oligotrophic gyres. Some  
157 | symbiont-barren species, such as *G. bulloides* and *N. pachyderma*, are optimized for survival in  
158 | regions with high productivity. Prey availability has also been shown to have a significant impact on  
159 | the distribution of foraminifera (Ortiz *et al.*, 1995; Watkins *et al.*, 1996; Watkins *et al.*, 1998). The  
160 | spinose species have calcareous spines that assist in prey capture and tend to be carnivorous or  
161 | omnivorous, feeding on copepods and other zooplankton; while the nonspinose species tend to prefer  
162 | phytoplankton (Spindler *et al.*, 1984).

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163 | Given the sensitivity of planktonic foraminifera to environmental change and their contribution to the  
164 | global carbonate flux, it is timely to address how the planktonic foraminifera could respond to  
165 | anthropogenic perturbations of the oceanic environment. Changes in the characteristics of planktonic  
166 | foraminiferal assemblages preserved in microfossil-rich sediments, and knowledge of the  
167 | ecophysiological traits of foraminifera species, has helped to reconstruct past environmental  
168 | conditions to as far back as 120 million years ago. Here, we reverse the problem and project the  
169 | future change by the end of the century in both i) the 3D biogeography of planktonic foraminifera  
170 | based on their physiological sensitivities to environmental conditions (temperature, food and light),  
171 | and ii) the carbon chemistry of their habitat with ocean acidification.

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## 172 | 2. Materials and methods

### 173 | 2.1. Earth system model and simulations

174 | To simulate the present-day and future global ocean environments we used the Institut Pierre-Simon  
175 | Laplace Coupled Model 4 (IPSL-CM4) model. The IPSL model couples the Laboratoire de  
176 | Météorologie Dynamique atmospheric model (LMDZ-4), with a horizontal resolution of about  $3 \times 2.5^\circ$   
177 | and 19 vertical levels (Hourdin *et al.*, 2006) to the OPA-8 ocean model, with a horizontal resolution of  
178 |  $2^\circ \times 2^\circ \cdot \cos\phi$ , 31 vertical levels and a surface ocean thickness of 10 m, and the LIM sea-ice model  
179 | (Madec *et al.*, 1998). The terrestrial biosphere is represented by the global vegetation model

203 ORCHIDEE (Krinner *et al.*, 2005) and the marine biogeochemical cycles by the PISCES model  
204 (Aumont *et al.*, 2003).

205 PISCES simulates the cycling of carbon, oxygen, and the major nutrients determining phytoplankton  
206 growth ( $\text{PO}_4^{3-}$ ,  $\text{NO}_3^-$ ,  $\text{NH}_4^+$ , Si, Fe). Phytoplankton growth is limited by the availability of **external**  
207 nutrients, **as well as** temperature, and light. The model has two phytoplankton size classes (small and  
208 large), representing nanophytoplankton and diatoms, as well as two zooplankton size classes (small  
209 and large), representing microzooplankton and mesozooplankton. The C:N:P ratios are assumed  
210 constant 122:16:1 (Anderson & Sarmiento, 1994), while the internal ratios of Fe:C, Chl:C, and Si:C of  
211 phytoplankton are predicted by the model. For more details on PISCES see Aumont and Bopp (2006),  
212 **and** Gehlen *et al.* (2006).

213 **To produce the simulations used here, the** IPSL model is forced with historical (1860–1999)  $\text{CO}_2$   
214 **emissions** (Marland and Andres, 2005) and the IPCC AR4 A2 high  $\text{CO}_2$  emission **future** (2000–2100),  
215 **scenario** (Nakicenovic *et al.* 2000). To calculate the input fields for the FORAMCLIM model (*i.e.* ocean  
216 temperature,  $T$ , total phytoplankton concentration,  $PHY$ , photosynthetically active radiation,  $PAR$ , and  
217 the carbonate ion concentration,  $\text{CO}_3^{2-}$ ) a monthly climatology is calculated by averaging the drift-  
218 corrected fields over **two** ten-year periods: present (2000–2009) and future (2090–2099). **These IPSL**  
219 **model simulations have been evaluated over the historical period** (Schneider *et al.*, 2008) and have  
220 **contributed to multimodel studies of the future change in marine primary productivity** (Steinacher *et*  
221 **al.**, 2010) and the carbon cycle (Roy *et al.*, 2011).

## 2.2. Foraminifera model (FORAMCLIM)

223 We use the FORAMCLIM model (Lombard *et al.*, 2011) to simulate the growth rates and the  
224 abundances of eight common and widely-studied foraminifera species. Five of the simulated species  
225 are spinose (*Orbulina universa*, *Globigerinoides sacculifer*, *Globigerinoides ruber*, *Globigerinella*  
226 *siphonifera*, *Globigerina bulloides*) and three species are nonspinose (*Neogloboquadrina dutertrei*,  
227 *Neogloboquadrina incompta*, *Neogloboquadrina pachyderma*). **The FORAMCLIM model incorporates**  
228 **i) the response of each species of foraminifera to multiple environmental drivers (food, temperature**  
229 **and light) and ii) the impact of these drivers on independent process (photosynthesis, nutrition and**

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240 respiration). Growth rates in the model are the result of the antagonism between food inputs (nutrition,  
 241 photosynthesis) and the physiological expenses of the organisms (respiration). For a full appreciation  
 242 of the model design, readers are encouraged to refer to the model description in Lombard *et al.*  
 243 (2011) and references therein.

244 The growth-rate relationships in FORAMCLIM were based on the observed physiological responses  
 245 of living specimens under controlled laboratory conditions (Lombard *et al.*, 2009a; Lombard *et al.*,  
 246 2009b; Lombard *et al.*, 2011). In FORAMCLIM, the daily growth rate  $\mu$  ( $d^{-1}$ ) is calculated as  $\ln(W_f/W_i)$ ,  
 247 where  $W_f$  and  $W_i$  are the final and initial weights of the foraminifera over a one day period. The  
 248 change in weight,  $\Delta W$ , ( $\mu g C d^{-1}$ )—that is, the species-specific change in weight of a 250  $\mu m$  individual  
 249 per day—is simulated based on three main physiological rates: nutrition ( $N$ ), respiration ( $R$ ) and  
 250 photosynthesis by the algal symbionts ( $P$ ).

$$251 \quad \Delta W(T, F, PAR) = N(T, F) + P(T, PAR) - R(T) \quad (1)$$

252 These physiological rates are a function of ocean temperature ( $T$ ), light ( $PAR$ , photosynthetically  
 253 active radiation) and food concentration ( $F$ ). Here, the total phytoplankton concentration ( $PHY$ ) is  
 254 used as a proxy for  $F$ , according to Lombard *et al.* (2011). We use the 3D decadal-mean climatologies  
 255 of  $T$ ,  $F$ , and  $PAR$  for present and future time slices of the IPSL model simulations.

256 The relationships between growth rates and abundances were calibrated against abundances  
 257 observed in multinet plankton tows (Lombard *et al.*, 2011). Based on the strong relationship between  
 258 physiological rates and abundances observed in multinet plankton tows, an exponential relationship  
 259 between abundance ( $Abund$ , individuals per  $m^3$ ) and  $\mu$  was assumed (Lombard *et al.*, 2011), where

$$260 \quad Abund = a \mu^b - a + 0.1 \quad (2)$$

261 Generally, the abundance, or standing stock in the water column, is given by the annual mean

$$262 \quad \sum_{t=1:12} \frac{Abund_i(t)}{12} dt$$

In the cases where we estimate the maximum abundance that could potentially

263 reach the ocean sediments, the monthly-mean depth-integrated abundances are integrated over the

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274 seasonal cycle  $\sum_{i=1:12} Abund_i(t)dt$ . The relative abundances,  $Rabund$ , for each species are

275 
$$Rabund_i = \frac{Abund_i}{\sum_{i=1:8} Abund_i} \times 100\%.$$

276 All the physiological parameters are species-specific. The most relevant parameters to this study are  
277 listed in Table 1. The contribution of photosynthetically-derived organic matter to the nutrition rate is  
278 set by both  $\%p$ , the fraction of the symbiont photosynthesis that is utilized in foraminiferal growth, and  
279  $s_{nb}$ , the number of algal symbionts per 250  $\mu\text{m}$  individual (Table 1). Photosynthesis only contributes to  
280 the growth rate in species that bear algal symbionts. The food-driven component of the foraminiferal  
281 nutrition rate is largely dependent on the half-saturation constant for the Michaelis-Menten  
282 relationship,  $k_n$ . Species with lower  $k_n$ , tend to be more adapted to oligotrophic waters, while species  
283 with high  $k_n$  tend to require higher food concentrations for growth.

### 284 2.3. Foraminiferal assemblage and calcite saturation data

285 For model evaluation we use two independent data sets: i) the surface abundances from global  
286 plankton tows (Bé & Tolderlund, 1971), and ii) the relative abundances from sediment top cores. The  
287 observed relative abundances of foraminifera in sediment cores (Figure S2a) are compiled from the  
288 MARGO database (Barrows & Juggins, 2005; Hayes *et al.*, 2005; Kucera *et al.*, 2004). Although the  
289 key focus of the MARGO database is the reconstruction of sea surface temperatures, the relative  
290 abundances are also available. We compiled all the available relative abundances in the MARGO  
291 database from the top cores and recalculated the relative abundances based on only the eight  
292 species used in this study.

293 The empirical relationships between foraminiferal growth rates and abundances in the FORAMCLIM  
294 model were originally calibrated against a compilation of multinet plankton tow data (Watkins *et al.*,  
295 1996; Watkins *et al.*, 1998; Schiebel *et al.*, 2001; Field, 2004; Kuroyanagi & Kawahata, 2004;  
296 Schiebel *et al.*, 2004), which is why we can't use this database to evaluate the model. We use the  
297 sampling sites from this same data set to characterize the carbonate chemistry of the present day  
298 potential habitat of foraminiferal species. Here we "sample" the observed calcite saturation state,  $\Omega_c$ .

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state  $\Omega_c = \frac{[Ca^{2+}][CO_3^{2-}]}{K_{sp}^{CaCO_3}}$ , where

$[Ca^{2+}]$  and  $[CO_3^{2-}]$  are the calcium and carbonate ion concentrations and  $K_{sp}$  is the stoichiometric solubility product of calcite ( $CaCO_3$ ). When  $\Omega_c$  is below the threshold of  $\Omega_c = 1$ , mineral calcite dissolves, while above it calcite remains stable. - ... [2]

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316 at the same locations (latitude, longitude, depth; Figure S2b) where foraminifera have been collected  
317 in multinet plankton tows (Watkins *et al.*, 1996; Watkins *et al.*, 1998; Schiebel *et al.*, 2001; Field, 2004;  
318 Kuroyanagi & Kawahata, 2004; Schiebel *et al.*, 2004).  $\Omega_C$  is calculated based on the GLODAP (Key  
319 *et al.*, 2004) and WOCE (World Ocean Circulation Experiment) databases. For each species of  
320 foraminifera we estimate the percentage of the abundance residing in waters of different  $\Omega_C$  ranges.

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#### 321 2.4. Model performance

322 The FORAMCLIM model captures the broadscale patterns of abundance and species dominance.  
323 The distributions of surface abundance from plankton tows (Bé & Tolderlund, 1971) are well captured  
324 by the model with the highest abundances in the tropics and subpolar regions and the lowest in the  
325 subtropics (Figure S3a). Yet, surface abundances tend to be overestimated, particularly in the  
326 subtropics. This is most likely due to the model being calibrated against multinet plankton tow data,  
327 which uses smaller mesh sizes (63–100  $\mu\text{m}$ ) relative to the 200  $\mu\text{m}$  used by Bé & Tolderlund (1971).  
328 Qualitatively, the dominant species (the species with the highest abundance) were also simulated well  
329 by the model with *G. bulloides* in the more productive upwelling areas and temperate zones, *G. ruber*  
330 in the subtropical gyres, *N. pachyderma* in the subpolar/polar regions and *G. sacculifer* dominating in  
331 the tropical/subtropical regions in between (Figure S3). The model reproduced 43% of the observed  
332 species dominance from surface plankton tow data (Table 2). This level of agreement is lower than  
333 the model-based and satellite-based estimates of Lombard *et al.* (2011) (Table 2) and is most likely  
334 due to the displacement of the simulated water masses and oceanic fronts relative to their real world  
335 counterparts, as is typical of Earth system models (Seferian *et al.*, 2013). Also some species have  
336 quite similar abundances locally, so small errors in abundance can lead to significant errors in species  
337 dominance.

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338 The relative abundances and diversity are well captured by the model with the relative abundance  
339 root mean square errors (RMSE) ranging between 3.2% and 24.1% and a diversity RMSE of 0.48  
340 (Table 2). For all species, except *N. pachyderma*, the relative abundance RMSEs are slightly larger  
341 than in Lombard *et al.* (2011), but smaller than in Fraile *et al.* (2008).

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346 In summary, there is a tendency to slightly overestimate the standing stock of foraminifera relative to  
347 the sparse surface plankton data, and to underestimate the changes in abundance in response to  
348 changing environmental conditions relative to observed abundances from sediment cores (Kageyama  
349 *et al.*, 2012).

### 350 *2.1. Modelling planktonic foraminifera: strengths and limitations*

351 The two most established approaches currently used to simulate the biodiversity of foraminifera are  
352 the ecophysiological approach used in this study, FORAMCLIM (Lombard *et al.*, 2011), and the  
353 ecosystem approach developed specifically to capture dynamic changes in planktonic foraminiferal  
354 populations, PLAFOM (Fraile *et al.* 2008). All approaches used for projecting climate impacts on  
355 marine biogeography have their unique set of strengths and weaknesses (Pereira *et al.*, 2010). One  
356 of the drawbacks of the dynamic ecosystem approach is that many processes (i.e. mortality,  
357 competition, and predation) are not well known (Hemleben *et al.*, 1989). Furthermore, the parameters  
358 that describe these processes can't be optimized independently using the data that is currently  
359 available. Another limitation of the Fraile *et al.* (2008) approach is that the depth profiles of  
360 foraminiferal abundance are not simulated. Capturing vertical changes is important if we want to  
361 estimate the impact of shifts in habitat preference on both the net foraminiferal abundance and the  
362 climate signals recorded by foraminiferal paleoproxies. Yet, the dynamical approach could be better  
363 adapted to simulate events controlled by population biology and hydrodynamics, which are known to  
364 be important in controlling foraminifera abundance and their flux to the deep ocean (De La Rocha &  
365 Passow, 2007), such as the pulsed fluxes of foraminiferal tests that can occur sporadically (Sautter &  
366 Thunell, 1991) or in short bursts in response to storms (Schiebel *et al.*, 2005), and the advection of  
367 empty tests from their production sites (Siegel & Deuser, 1997; von Gyldenfeldt *et al.*, 2002).

368 One of the attractive aspects of the FORAMCLIM model is that it is empirically-based. The  
369 relationships between environmental conditions (i.e. light, temperature) and foraminiferal growth rates  
370 are derived under controlled laboratory conditions. Since it is impossible, based on the available  
371 knowledge, to incorporate the influence of all ecological and physiological processes on foraminiferal  
372 abundance, the relationships between growth rates and abundance are calibrated against the  
373 standing stock of foraminifera from multinet plankton tows; effectively allowing us to bridge this

374 sizeable knowledge gap. The parameters of this calibration integrate the influence of the processes  
375 unresolved by the model. By applying the foraminifera model to climate simulations we can project  
376 these observation-based relationships into the future.

377 Critical to reliable model performance is that these model relationships are realistic. Here we  
378 elaborate on a previous discussion of the strengths and limitations of the FORAMCLIM model  
379 (Lombard *et al.*, 2011). First, the laboratory-based growth rate relationships may not hold for the real  
380 ocean. The laboratory experiments were conducted on specific specimens whose response to  
381 environmental perturbations may not be representative of the global population—similar to the  
382 responses that have been observed for different strains of coccolithophore species in response to  
383 changes in carbonate concentration (Ridgwell *et al.*, 2009; Langer *et al.*, 2009). Also, foraminifera in  
384 the laboratory could be more sensitive to perturbations in environmental conditions than in their  
385 natural habitat. It hasn't been possible to reproduce planktonic foraminifera in the laboratory, which is  
386 one indication that foraminifera in the laboratory are not behaving as they would in their natural  
387 environment. Furthermore, the physiological responses of foraminifera in the laboratory could be  
388 more related to stress than to environmental perturbations. It is important to keep in mind that  
389 although all physiological laboratory experiments are artificial, they are currently the most direct  
390 approach available for quantifying the growth response of foraminifera to specific environmental  
391 changes.

392 Another potential weakness is that the relationships between the abundances and the growth rates  
393 are weakly correlated (Lombard *et al.*, 2011). This could partly be due to each morphological species  
394 being a combination of cryptic species, each with distinct habitat preferences and responses to  
395 environmental change (de Vargas *et al.*, 2002). A convincing explanation for the weak relationship  
396 between biomass and abundance could be related to the FORAMCLIM model not resolving variations  
397 in shell size: a wide range of abundances can be fitted to the same total biomass of a foraminiferal  
398 population depending on how this biomass is distributed over different size classes. To illustrate this  
399 point, we can take the typical biomass size spectrum from Schiebel and Mollevan (2012): a 1 m<sup>3</sup> of  
400 water with a foraminiferal abundance of 100 individuals m<sup>-3</sup> is grouped into 3 size classes 100–150  
401 μm, 150–250 μm, and 250+ μm with each size class having 75, 19 and 6 individuals respectively. A  
402 small change in the size spectrum (e.g. having just two more individuals in the largest and

403 intermediate size classes (i.e. 21, 8 individuals each) would require a large decrease in the total  
404 abundance from 100 to 68 individuals to match the same total biomass.

405 Another limitation of the FORAMCLIM model is that it currently includes only the species on which  
406 sufficient physiological laboratory experiments have been conducted. That is, 8 of the approximately  
407 50 species of morphologically-distinct planktonic foraminifera. Therefore, it can't be used to estimate  
408 the total (i.e. all species) foraminiferal abundance, diversity or carbonate production. Nevertheless,  
409 based on sediment top-core samples (Kucera et al., 2004), the 8 species currently represented in the  
410 FORAMCLIM model account for a large proportion of the total abundance (about 50%).

### 411 3. Results

#### 412 3.1. Future changes in abundance and diversity

413 Under climate change, temperature, food availability and light were perturbed such that the total  
414 foraminiferal abundance (combined abundance of the eight species in the FORAMCLIM model, Figure  
415 1a) shifted polewards from the tropics to the subtropics, while abundance decreased in the subpolar  
416 regions (Figure 1b) by the end of the century. The simulated depth-integrated abundance reduced by  
417 up to 40% in the tropics and subpolar regions and increased by greater than 100% in the subtropics.  
418 Throughout the tropics the total abundance (Figure 1c) shifted deeper in the water column (Figure  
419 1d), reducing the total abundance of foraminifera at the ocean surface by more than 50% (>10 ind m<sup>-3</sup>,  
420 Figure 2b). Under climate change the pattern of foraminiferal diversity (Figure 2c) responded  
421 similarly to that of abundance: it decreased in the tropics, increased in the subpolar regions (Figure  
422 2d) and shifted to depth in the tropics (not shown). The decreased diversity in the tropics is primarily  
423 due to the local disappearance of *G. siphonifera* and *N. dutertrei*.

424 In the simulation, three species dominated the changes in total foraminiferal abundance: the two  
425 abundant warm-water species—*G. ruber* and *G. sacculifer*—drove the reduction in total abundance in  
426 the tropics and the increase in the subtropics, while *N. pachyderma* dominated the reduction in the  
427 high latitudes and the small increases in abundance around the poles (Figures 3a and 3b). In the  
428 tropics, the climate-driven reductions in the distribution of *G. ruber* and *G. sacculifer* were similar in

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431 magnitude (5 ind m<sup>-3</sup>), and each integrated to a more than 100 ind m<sup>-2</sup> reduction over the whole water  
432 column (Figure 3b). In the high-latitudes, the poleward shift in abundance of *N. pachyderma* reduced  
433 the net abundance in surface waters (~4 ind m<sup>-3</sup>) and throughout the water column (~200 ind m<sup>-2</sup>, not  
434 shown).

435 The changes in relative abundance are also presented, since this is what is measured in sediment  
436 cores. In the tropics, despite the large decreases in the abundances of the two dominant species (*G.*  
437 *ruber* and *G. sacculifer*), their relative abundances at the ocean surface increased (Figure 3c) and the  
438 depth-integrated relative abundances changed very little (Figure 3d). In the mid latitudes (10°–40°)  
439 the abundance and relative abundance of *G. bulloides*, *N. incompta* and *N. dutertrei* decreased, while  
440 *G. sacculifer* and *G. ruber* increased. In the high latitudes (>50°), where the species diversity is much  
441 lower than in the tropics (Figure 2c), the changes in abundance ~~resulted in changes~~ in the relative  
442 abundance ~~that can interpreted more easily~~. Although the abundance of *G. bulloides*, *N. incompta* and  
443 *N. dutertrei* barely changed (Figure 3a and 3b), the large decrease in the abundance of the dominant  
444 species, *N. pachyderma*, drove a substantial increase in the relative abundance of these species  
445 (Figure 3c and 3d). ~~The more even distribution of abundance between the species~~ resulted in an  
446 overall increase in ~~the diversity index~~ in the higher latitudes (Figure 2d).

### 447 3.2. Environmental drivers of foraminiferal biogeography

448 ~~It is not directly possible to separate the impact of temperature and food on foraminiferal distributions~~  
449 ~~in nature, so we turn to the model to attempt to explore the potential relative impacts of projected~~  
450 ~~changes in food, temperature and light on future foraminiferal distributions. An advantage of the~~  
451 ~~FORAMCLIM model is the ease with which the various drivers of the changes in abundance can be~~  
452 ~~disentangled~~. By systematically allowing only one parameter to vary, we can partially separate the  
453 total change in foraminiferal abundance into components driven by each of the environmental  
454 drivers—temperature, food and light. ~~Given the paucity of data for the evaluation of these simulated~~  
455 ~~responses, these results should be regarded as initial sensitivity experiments. The future change in~~  
456 ocean temperature (Figure 4) is the primary driver of the change in the basin-scale biogeography of  
457 foraminifera (Figure 5), ~~followed by food availability (Figures 4,5)~~. Changes in light availability have a  
458 minor impact (not shown).

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474 | Temperature was the dominant driver of the poleward shift of foraminifer~~al~~ abundance from the  
475 | tropics (Figure 5a). The 1–3°C increase in sea surface temperatures in the tropics and subtropics  
476 | (Figure 4a) throughout the water column (Figure 4b) decreased the habitat suitability in the tropical  
477 | waters—the waters became too warm for optimal foraminifer~~al~~ growth—yet increased the habitat  
478 | suitability in the subtropics (Figure 5a) and in the deeper waters of the tropics (Figure 5b).

479 | In the subpolar and polar regions, where *N. pachyderma* dominates (Figure 3a,b), the shift in  
480 | abundance was a combined response to temperature and food-driven changes in nutrition rates  
481 | (Figure 5a and 5c respectively). The broadscale patterns, the subpolar decrease and polar increase in  
482 | abundance (Figure 5a,b), ~~were~~ driven by temperature (Figure 4a). Yet, increases in phytoplankton  
483 | concentration in localized patches, ~~particularly in the Southern Ocean~~ (Figure 4c), and in subsurface  
484 | waters (Figure 4d) drove increases in abundance (Figures 5c and 5d). ~~The increase in phytoplankton~~  
485 | ~~abundance in the Southern Ocean is a shared feature of many future climate change simulations and~~  
486 | ~~is explained by the alleviation of light and iron limitation on phytoplankton growth (Steinacher et al.,~~  
487 | ~~2010).~~ The food-driven increases in the ~~foraminiferal~~ abundance tended to offset the temperature-  
488 | driven reductions. Other areas ~~with similar~~ offsets include large patches throughout the North Atlantic  
489 | and the Equatorial and coastal upwelling regions.

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### 490 | 3.3. *Species abundance and potential suitable habitat*

491 | To assess the species-specific vulnerability of foraminifera to climate change we calculated the  
492 | percent change in the globally-averaged species abundance and potential suitable habitat (Figure 6),  
493 | where the potential habitat is defined as anywhere where the environmental conditions (i.e.  
494 | temperature, food and light conditions) are sufficient for foraminifer~~al~~ growth. Some species 'profited'  
495 | (*O. universa*, *G. sacculifer*, *G. siphonifera* and *G. ruber*); that is their potential habitat increased by  
496 | between 5% and 20%. ~~Whilst~~ higher-latitude species were more vulnerable (e.g. *N. incompta*, *N.*  
497 | *pachyderma*): their potential habitat and net abundance decreased by between 10% and 40%. For *G.*  
498 | *siphonifera* the potential habitat increased but the abundance decreased.

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### 3.4. Carbon chemistry of the foraminiferal habitat

Although we don't explicitly account for the impact of ocean acidification on either foraminiferal calcification or physiological processes in the current version of the FORAMCLIM model, we can make an assessment of the potential impacts by quantifying the predicted changes in the carbonate concentration  $[\text{CO}_3]^{2-}$  and calcite saturation state,  $\Omega_c$ , within the habitat range of each species of foraminifera.

First, we would like to have an indication of the present-day distribution of foraminiferal abundance within waters of different  $\Omega_c$  classes. We find that only a very small proportion of the abundance of all the foraminiferal species resides in waters with  $\Omega_c$  less than 2, even though substantial volumes of water with low  $\Omega_c$  are sampled, particularly in the northern high latitudes (Figure 7). The highest foraminiferal abundances from the multinet plankton tows were sampled in waters with  $3 < \Omega_c < 6$ .

Second, we project how the carbonate chemistry of foraminiferal habitat changes by the end of this century. Calcite saturation states decrease throughout the global ocean and waters with low saturations states ( $\Omega_c < 2$ ) shoal (Figure 8a,b) and become more widespread across the surface ocean. Most surface waters polewards of  $40^\circ$  have  $\Omega_c < 2$ . Virtually none of the simulated present-day foraminiferal habitat has ambient  $\Omega_c < 2$ . Yet, by the end of the century between 10% and 95% of the habitats of most foraminiferal species have an  $\Omega_c < 2$  (Figure 8c). High latitude species, *N. pachyderma* and *N. incompta*, are potentially most vulnerable, with some of their suitable habitat even becoming undersaturated ( $\Omega_c < 1$ ) with respect to calcite by the end of the century (when  $\Omega_c$  is below the threshold of  $\Omega_c = 1$ , mineral calcite becomes unstable). Also, the carbonate ion concentrations of the potential foraminiferal habitat decrease to between 20 and 70  $\mu\text{mol kg}^{-1}$ , with the largest reductions in the equatorial regions (Figure 8d).

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538 4. Discussion

539 4.1. Climate impacts

540 It is unclear how vulnerable specific foraminiferal species may be to anthropogenic climate change.  
541 Since the last substantial extinction event in the Pliocene the modern assemblage of species has  
542 remained relatively stable under glacial-interglacial fluctuations (Jackson & Sheldon, 1994). Yet, the  
543 oceanic environment is fast approaching conditions that are well outside those of glacial-interglacial  
544 cycles. It is expected that pelagic species, and in particular planktonic species, will have the potential  
545 to escape some climatic changes by shifting their populations to regions with more favorable  
546 conditions (Burrows *et al.*, 2011), as predicted here for species such as *G. sacculifer* and *G. ruber*. Yet,  
547 we show that the available potential habitat is reduced for high latitude species, such as *N.*  
548 *pachyderma*, and that this reduction is associated with a drop in the net global abundance. For one  
549 species, *G. siphonifera*, the suitable habitat range increases, yet its net global abundance decreases.  
550 Such an increase in habitat range without similar increases in abundance indicates that temperature,  
551 light and food availability are perturbed such the species can exist over a greater habitat range, but  
552 that the overall environmental conditions are suboptimal for foraminiferal growth.  
553 Based on the FORAMCLIM simulations, it would be expected that anthropogenically-driven shifts in  
554 the basin-scale biogeography of foraminifera should be observable (Figure 3 a,b). But, in sediment  
555 samples, the changes in the relative abundances in some regions, particularly the tropics, may be too  
556 small to detect (Figure 3d). Furthermore, shifts in the species abundance can cause non-intuitive  
557 shifts in the relative abundance, particularly in regions of high species diversity such as the tropics.  
558 Yet, in the high latitudes, where the diversity is lower (Figure 2d), the interpretation of the changes in  
559 relative abundance should be simpler.  
560 We have shown that climate change is projected to alter the temperature, food and light conditions  
561 that influence foraminiferal growth rates and, consequently, shift both the vertical and geographical  
562 distributions of foraminiferal abundance/diversity (Figures 1 & 2). In the tropics/subtropics, the  
563 changes in abundance are driven by the regionally dominant species: *G. ruber* and *G. sacculifer*.  
564 Here, temperature (Figure 4) dominates the geographical shifts in foraminiferal abundance, while

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572 multiple drivers (phytoplankton and temperature) cause the vertical shifts (Figure 5). On the contrary,  
573 in the polar/subpolar regions food availability and temperature drive the geographical shifts in  
574 foraminiferal abundance, while mostly changes in phytoplankton concentrations drive the vertical  
575 shifts. The changes in the abundance of foraminifera are associated with *N. pachyderma* and are in  
576 agreement with observational studies (Fairbanks & Wiebe, 1980; Kohfeld *et al.*, 1996; Kuroyanagi &  
577 Kawahata, 2004; Bergami *et al.*, 2009) that demonstrate that the geographical distribution was  
578 primarily controlled by ocean temperatures, while the vertical distribution was controlled by the depth  
579 of the chlorophyll maximum and the pycnocline. Light doesn't produce a strong change in abundance  
580 in our simulations and is therefore not discussed here. In reality, however, the response of symbiont-  
581 bearing foraminifera to light is likely to be much more complex than simulated in the foraminifera  
582 model.

583 The drivers of vertical and horizontal distributional changes can differ because food, light and  
584 temperature may have impacts on foraminiferal abundances that are uncorrelated: they either act to  
585 reinforce or counteract each other's impact on foraminiferal abundances. Also, the drivers themselves  
586 may not be well correlated. Under climate change, Earth system models simulate increases in ocean  
587 temperature in most regions, yet PP can either decrease or increase (Steinacher *et al.*, 2010).  
588 Furthermore, the nutritional requirements of each species is unique representing the different  
589 strategies that foraminifera use to feed and grow. Symbiotic species have a strong dependence on  
590 light availability. Therefore they mostly display horizontal effects and vertical shifts that are restricted  
591 to the euphotic zone (up to about 200 m). Species without symbionts can display less restricted  
592 vertical responses because they don't rely directly on light. They can travel as deep as the food  
593 source. Species with a stronger prey dependency are more likely to be more sensitive to changes in  
594 the availability of prey than temperature. This complexity is taken into account in the  
595 ORCA/PISCES/FORAMCLIM models. For example, in the high latitudes, the dominant species here,  
596 *N. pachyderma* drives much of the change in the simulated total foraminiferal abundance. It's  
597 abundance is reduced throughout most of it's habitat range in response to a warming ocean, but it's  
598 abundance increases over patches of the ocean, and shifts to depth in some regions, in response to  
599 an increase in food availability. By contrast, in tropics/subtropics the dominant species *G. sacculifer*  
600 and *G. ruber* shift polewards and deeper in the water column both as the thermocline and nutricline

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609 | deepen, yet food availability does not contribute to the latitudinal shifts because the column-integrated  
610 | food availability is not altered significantly throughout the habitat range.

611 | We show that climate change could result in vertical shifts in foraminiferal abundance that are driven  
612 | by either or both food availability and temperature. Interestingly, comparable vertical shifts in  
613 | foraminiferal abundance over glacial-interglacial time periods may complicate the reconstruction of  
614 | sea-surface temperatures from foraminiferal microfossil deposits: in paleoclimate reconstructions the  
615 | vertical distributions foraminifera are generally assumed to be stationary over time (e.g. Kucera et al.,  
616 | 2005).

617 | Opinions differ on the relative impacts of food availability, temperature or other environmental factors  
618 | on the distribution of planktonic foraminifera. Although it is generally accepted that at the extremes of  
619 | a species temperature tolerance, temperature drives the changes in the geographical extent of  
620 | foraminifera (Rutherford *et al.*, 1999), each species' preferred temperature range is broad. Within  
621 | these temperature ranges it has been shown that regional patterns of abundance are strongly  
622 | correlated with specific-specific responses to food, light (Ortiz *et al.*, 1995; Watkins *et al.*, 1996; Field,  
623 | 2004) salinity, and turbidity (Retailleau *et al.*, 2011). On the contrary, it could be argued that food  
624 | availability is generally adequate to maintain foraminiferal populations and that changes in abundance  
625 | are primarily temperature-driven. A database of time series of abundance/assemblage data and  
626 | concomitant environmental measurements of temperature, food and light would be an invaluable  
627 | resource for the evaluation of the drivers of the simulated changes in the distributions of foraminiferal  
628 | abundance.

629 | The simulated response of foraminiferal diversity to climate change may differ significantly if all extant  
630 | species could be included in the model. For example, tropical species present in low concentrations,  
631 | but excluded in this analysis, could flourish as temperatures increase. Also, the vertical stratification of  
632 | large regions of the global ocean should increase with climate change (Sarmiento *et al.*, 2004), which  
633 | can increase vertical niche separation thereby allowing a greater diversity of species to subsist (Al-  
634 | Saboui *et al.*, 2007). By including more species in the FORAMCLIM model, these effects could  
635 | counteract the simulated decrease in diversity in the tropics. Another important factor that will  
636 | influence how diversity responds to climate change is that most foraminiferal morphospecies have

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652 many genotypes that exhibit specific ecology, habitat preferences and biogeography (Aurahs *et al.*,  
653 2009). A potential approach to incorporate more species diversity, and to partially circumvent the lack  
654 of information on key ecological and physiological processes for many *foraminiferal* species, would be  
655 to apply the self-assembling biodiversity approach (Follows *et al.*, 2007) to simulate more complex  
656 *foraminiferal* assemblages.

#### 657 4.2. *Calcification and acidification impacts*

658 If net calcification were to scale directly with *foraminiferal* abundance, the large-scale rearrangements  
659 in abundance with climate change would *alone* cause significant changes in regional carbonate  
660 production. *For example, in the tropics/subtropics the 40% decrease in total simulated foraminiferal*  
661 *abundance could produce a 20% reduction in total planktic foraminiferal carbonate production, given*  
662 *that the 8 species in the FORAMCLIM model account for about 50% of the total planktonic*  
663 *foraminiferal abundance observed in the sediment core-tops (Kucera *et al.*, 2004). Such population–*  
664 *driven impacts on carbonate production could be further amplified or dampened if calcification rates*  
665 *themselves are impacted by anthropogenic change. Ocean acidification and the associated decrease*  
666 *in carbonate ion concentrations can alter* foraminiferal calcification rates (Lombard *et al.* 2010; Keul *et*  
667 *al.*, 2013), while higher ocean temperatures could accelerate calcification rates within certain  
668 temperature windows.

669 With future increases in atmospheric CO<sub>2</sub>, we show that the carbonate concentration of the preferred  
670 habitat range of planktonic foraminifera decreases zonally from 10–30 μmol kg<sup>-1</sup> in the polar/subpolar  
671 regions to 30–70 μmol kg<sup>-1</sup> in the subtropical/tropical regions by the end of this century (Figure 8d).  
672 Even without dropping below the calcite saturation state, such changes in carbonate ion concentration  
673 may have significant impacts on *foraminiferal* tests. Evidence exists for shell thinning in foraminifera  
674 over recent (de Moel *et al.*, 2009; Moy *et al.*, 2009) and geological timescales (Barker & Elderfield,  
675 2002) and it has been suggested that these changes are a response to higher atmospheric CO<sub>2</sub>  
676 concentrations and the reduction of carbonate ion concentrations (Keul *et al.*, 2013). Such as for other  
677 calcifying planktonic species (Riebesell *et al.*, 2000; Zondervan *et al.*, 2001; Fabry *et al.*, 2008;  
678 Comeau *et al.*, 2010), the calcification by foraminifera is sensitive to changes in the carbonate ion  
679 concentration both in their natural environment (Beer *et al.*, 2010) and in laboratory cultures (Spero *et*

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699 *al.*, 1997; Bijma *et al.*, 1999; Bijma *et al.*, 2002; Russell *et al.*, 2004; Beer *et al.*, 2010; Lombard *et al.*,  
700 2010; Manno *et al.*, 2012; Keul *et al.*, 2013).

701 Despite the uncertainties associated with foraminiferal calcification, it is interesting to have a sense of  
702 the magnitude of the change in calcification that could be expected by applying laboratory-derived  
703 relationships (i.e. calcification vs carbonate ion concentration) from the literature to the foraminiferal  
704 distributions and the carbonate ion concentrations simulated here. For example, in a series of  
705 laboratory experiments, a reduction of 30–40  $\mu\text{mol kg}^{-1}$  in the carbonate ion concentration was  
706 associated with a 21–30% reduction in the calcification rates of *N. pachyderma* (Manno *et al.*, 2012).  
707 The reduction in the carbonate ion concentration throughout the habitat of *N. pachyderma* is projected  
708 to be  $\sim 30 \mu\text{mol kg}^{-1}$  (Figure 8d) and by crude extrapolation, we could expect a similar >20% drop in  
709 the net *N. pachyderma* foraminiferal carbonate flux in the high-latitudes due to ocean acidification by  
710 the end of this century. This reduction would reinforce the reduction in carbonate production due to  
711 the net climate-driven decrease in abundance of this species throughout its habitat range (Figures 3b,  
712 6). Similarly, based on the observed changes in the calcification rates of *G. sacculifer* with carbonate  
713 ion concentration (Bijma *et al.*, 2002; Lombard *et al.*, 2010, see equation 3), the projected reduction of  
714 up to 70  $\mu\text{mol kg}^{-1}$  in the carbonate ion concentration in the tropical/subtropical habitat range of *G.*  
715 *sacculifer* (Figure 8d) could result in an up to 10% reduction in the calcification rates of this species.  
716 Again, this would reinforce the reduction in carbonate production associated with the decrease in the  
717 abundance of this species throughout the tropics (Figure 3b), yet would counteract the increase in  
718 carbonate production associated with enhanced abundance in the subtropics.

719 In the polar/subpolar regions *N. pachyderma* dominates the assemblages (Figure S3b). The tests of  
720 *N. pachyderma* are expected to be most vulnerable to dissolution because the polar regions have  
721 lower carbonate ion concentrations and are consequently closer to the threshold of calcite saturation  
722 ( $\Omega = 1$ ). We show that by the end of the century, most of the habitat of high-latitude species drops  
723 below the calcite saturation state of 2 with greater than 10% of the potential habitat of the dominant  
724 high-latitude species, *N. pachyderma*, residing below the saturation horizon (Figure 8c), which could  
725 result in shell dissolution throughout this range.

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737 Although calcification by foraminifera is directly influenced by  $\text{CO}_3^{2-}$ , many other environmental factors  
 738 besides ambient carbonate ion concentrations influence the shell weight (de Villiers, 2004) including  
 739 temperature (Hemleben *et al.*, 1989; Manno *et al.*, 2012), light (Spero, 1992; Lombard *et al.*, 2010),  
 740 growth potential (Aldridge *et al.*, 2012). Clearly, the environmental controls on calcite production by  
 741 foraminifera are still poorly understood. A complex intra- and interspecies-specific interplay of factors  
 742 drive foraminiferal shell weights (Beer *et al.*, 2010). Both the magnitude and the sign of the slope of  
 743 the relationships between shell weight and carbonate ion concentrations vary between and within a  
 744 species (Keul *et al.*, 2013), and they vary widely depending on whether the relationships were based  
 745 on plankton tows (Beer *et al.*, 2010), top core sediments (Barker & Elderfield, 2002), or laboratory  
 746 cultures (Bijma *et al.*, 1999; Bijma *et al.*, 2002). A quantitative assessment of the impact of  
 747 acidification on the foraminiferal carbonate flux can be made with confidence only once these  
 748 complexities have been taken into account.

749 To quantify the foraminiferal carbonate flux, further model development should be encouraged,  
 750 particularly the incorporation of enhanced species diversity, shell calcification processes, and  
 751 empirical relationships between environmental conditions and foraminiferal size. Ideally, future  
 752 models will also incorporate the physiological response of foraminiferal calcification to multiple  
 753 environmental drivers.

#### 754 4.3. Future challenges

755 The challenge remains to observationally evaluate how well foraminifera models capture changes in  
 756 abundance in response to environmental change. There is little large-scale observational evidence for  
 757 historical trends in foraminiferal abundance and diversity over the period of anthropogenic climate  
 758 change. Large-scale changes in foraminiferal abundance have been observed in continuous plankton  
 759 records over the last five decades in the North Atlantic that are intriguingly similar to our simulations  
 760 (McQuatters-Gollop *et al.*, 2010), with large increase in the frequency of occurrence between 40°N  
 761 and 60°N. But further analysis of this data set is required before a quantitative assessment can be  
 762 made. Changes in species composition in response to anthropogenic climate change have been  
 763 observed in the sediment record of the Santa Barbara basin (Field *et al.*, 2006). It was shown that

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783 historical warming trends were associated with an increase in the abundance of tropical/subtropical  
784 species, and a decrease in subpolar/polar species (i.e. *N. pachyderma*) over the 20<sup>th</sup> century.

785 Ideally, the FORAMCLIM simulations should be tested against present-day time series of planktonic  
786 abundance and the key environmental variables such as temperature, phytoplankton concentration  
787 and light. For future studies, there are several instrumental records that should become available and  
788 provide an invaluable resource to improve our understanding of the environmental controls on the  
789 biogeography of foraminifera, including data collected with: i) plankton tows, ii) sediment traps (Zaric  
790 *et al.*, 2005), iii) sediment cores, and iv) continuous plankton recorders (CPR).

791 The plankton tow data used here, for the construction of the empirical relationships between  
792 physiological growth rates and abundances, represent only a subsample of what should become  
793 available in the future. More studies of historical trends in the assemblage of planktonic foraminifera  
794 deposited in ocean sediments, such as that of Field *et al.*, (2006), would be invaluable for evaluating  
795 the longer-term responses of species assemblages to climate change. Yet, such studies are restricted  
796 to ocean sediment cores from locations with high sedimentation rates and sufficient temporal  
797 resolution to determine historical trends. These would not be expected to provide the spatial coverage  
798 required for the basin-scale evaluation of global models. CPR records provide long time series of  
799 plankton diversity, yet unfortunately, we found that the routine preservation protocol used to store  
800 CPR samples did not preserve foraminifera well enough to determine relative abundances or shell  
801 weights. Only the most robust individuals were preserved and even their shells were found to be  
802 brittle and difficult to speciate. Another potential complication, with foraminiferal CPR data is that the  
803 sample may not represent the mean surface ocean distribution of foraminifera because i) the CPR  
804 does not resolve different water depths, and ii) the large mesh size (>200 μm) means that the smaller  
805 fraction of the foraminiferal fauna is not captured in the samples. Nevertheless, by taking the statistics  
806 of the CPR sampling protocol into account, it should be possible to use the total abundance of  
807 foraminifera recorded in the original written records for each CPR sample to evaluate the simulated  
808 changes in total foraminiferal abundance from the model.

809 Sedimentary paleorecords over glacial/interglacial timescales may be useful analogs for historical  
810 climate change. Yet, it can be difficult to know which combination of species is driving the observed

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821 changes in relative abundance. The differential dissolution of foraminifera in the sediments further  
822 complicates the interpretation of the signals recorded here. Also, we don't have direct measurements  
823 of the key environmental drivers of foraminiferal abundance — temperature, light, food availability—  
824 back through time, and must draw on proxy-based estimates of these quantities, which are plagued  
825 by similar uncertainties, and the proxies themselves are often based on foraminifera.

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826 Improved skill in representing the simulated responses of foraminiferal growth and abundance to  
827 environmental change and variability in models will increase our confidence in both future projections  
828 of foraminiferal biogeography and the reconstructions of past climates. Subsequent studies should  
829 focus on i) the continued sampling of foraminiferal diversity, abundance, and shell size and  
830 concomitant biophysical parameters to quantify changes in their distributions in response to  
831 environmental perturbations, and ii) evaluating the detectability of large-scale biogeographical shifts  
832 driven by climate-change given the natural variability in foraminiferal distributions. Given that the  
833 distributions of foraminifera are one of the most well known of all the taxa in the pelagic ocean and the  
834 feasibility of monitoring the large-scale changes in foraminifera, we have confidence that ongoing  
835 model-data syntheses should lead to detection and attribution of anthropogenically-driven changes in  
836 large-scale planktonic foraminiferal distributions.

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## 6. Tables

**Table 1.** Key species-specific parameters used in the FORAMCLIM model. The half saturation constant for the Michaelis-Menten relationship that describes the influence of food availability on the nutrition rate,  $k_n$ ; the fraction of the symbiont photosynthesis that is utilized in foraminiferal growth, % $p$ ; and the number of symbionts per individual 250  $\mu\text{m}$  foraminifer,  $s_{nb}$ .

|                       | $k_n$ ( $\mu\text{gC L}^{-1}$ ) | % $p$ | $s_{nb}$ |
|-----------------------|---------------------------------|-------|----------|
| <i>O. universa</i>    | 1.73                            | 0.46  | 716      |
| <i>G. sacculifer</i>  | 1.32                            | 0.40  | 1160     |
| <i>G. siphonifera</i> | 1.19                            | 0.30  | 720      |
| <i>G. ruber</i>       | 0.51                            | 0.37  | 1104     |
| <i>N. dutertrei</i>   | 1.00                            | -     | -        |
| <i>G. bulloides</i>   | 6.84                            | -     | -        |
| <i>N. incompta</i>    | 3.33                            | -     | -        |
| <i>N. pachyderma</i>  | 4.70                            | -     | -        |

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**Table 2.** Assessment of the simulated distribution of foraminiferal species (percentage of area with model-data agreement) using the plankton tow data of Bé and Tolderlund (1971). The RMSE of diversity and relative abundance are assessed against the MARGO top-core data. *Lombard*<sup>1</sup> is the model-based (FORAMCLIM) estimate from Lombard *et al.* (2010); *Lombard*<sup>2</sup> refers to the satellite-based estimate from Lombard *et al.* (2010); *Fraile*<sup>1</sup> refers to the model-based (PLAFOM) estimate from Fraile *et al.* (2008).

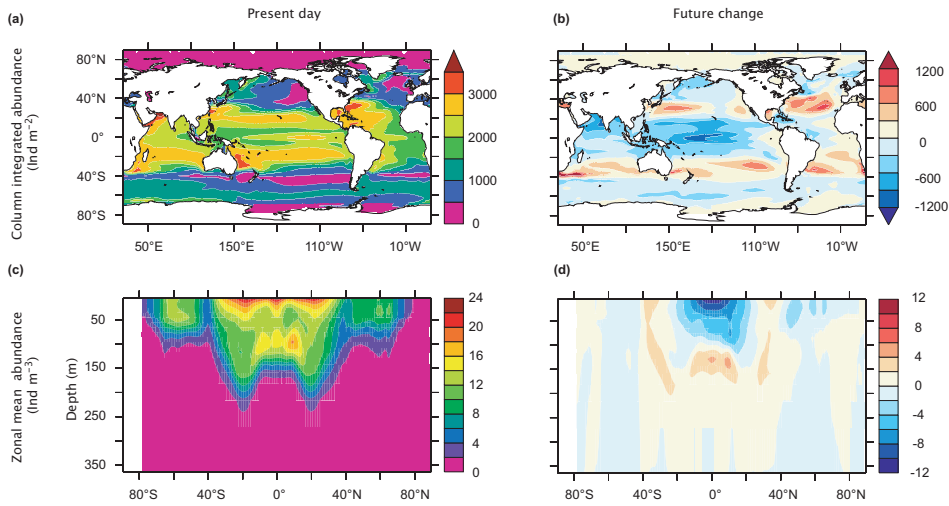
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|                           | This study | Other studies               |                             |                            |
|---------------------------|------------|-----------------------------|-----------------------------|----------------------------|
|                           |            | <i>Lombard</i> <sup>1</sup> | <i>Lombard</i> <sup>2</sup> | <i>Fraile</i> <sup>1</sup> |
| Dominant species (%)      | 43%        | 59%                         | 71%                         |                            |
| Diversity (RMSE)          | 0.56       | 0.48                        | 0.52                        |                            |
| Relative abundance (RMSE) |            |                             |                             |                            |
| <i>O. universa</i>        | 3.2        | 3.24                        | 3.28                        | -                          |
| <i>G. sacculifer</i>      | 12.1       | 12.38                       | 17.46                       | 23                         |
| <i>G. siphonifera</i>     | 6.1        | 5.29                        | 6.00                        | -                          |
| <i>G. ruber</i>           | 24.1       | 23.14                       | 17.76                       | 25                         |
| <i>N. dutertrei</i>       | 18.3       | 17.53                       | 17.23                       | -                          |
| <i>G. bulloides</i>       | 22.0       | 21.02                       | 18.97                       | 25                         |
| <i>N. incompta</i>        | 16.2       | 15.85                       | 14.85                       | 22                         |
| <i>N. pachyderma</i>      | 20.6       | 17.01                       | 12.32                       | 9                          |

## 7. Figures

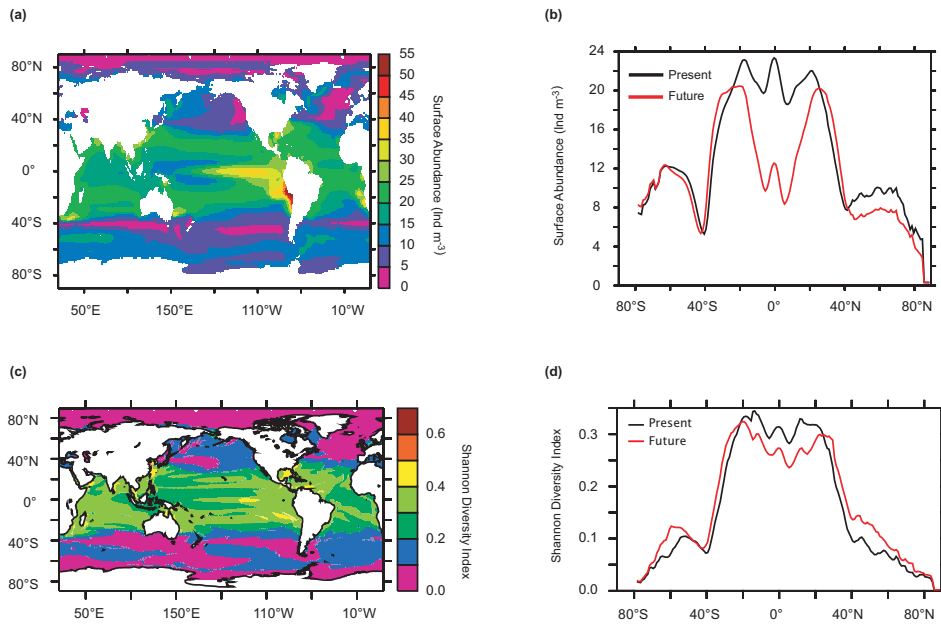
**Figure 1**

Present (a,c) and future changes (b,d) in the total simulated abundance (all species). (a,c) column-integrated abundance ( $\text{Ind m}^{-2}$ ), and (b, d) zonal-mean abundance ( $\text{Ind m}^{-3}$ ).



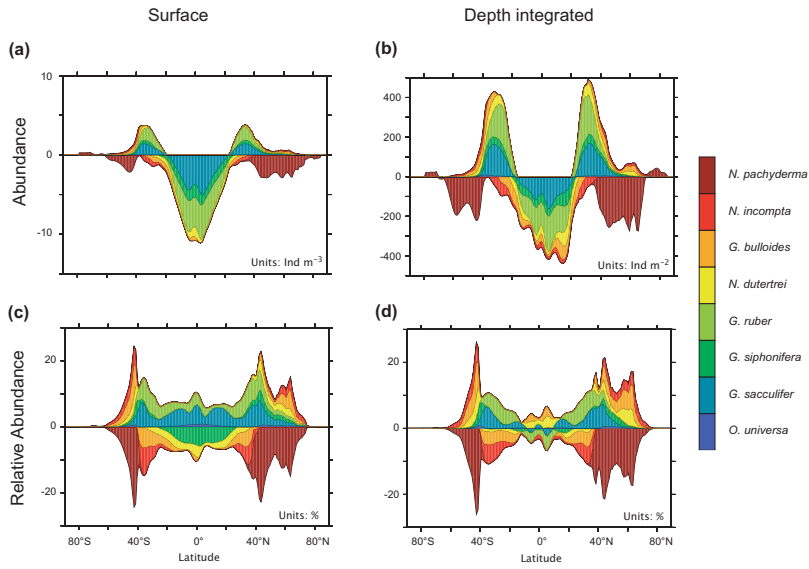
**Figure 2**

Total surface abundance of foraminifera ( $\text{Ind m}^{-3}$ ): (a) present-day surface distribution, and (b) zonally-averaged surface abundance for the present-day and the future. Shannon diversity index of the simulated foraminifera: (c) surface distribution, and (d) zonally-averaged for the present-day and future.



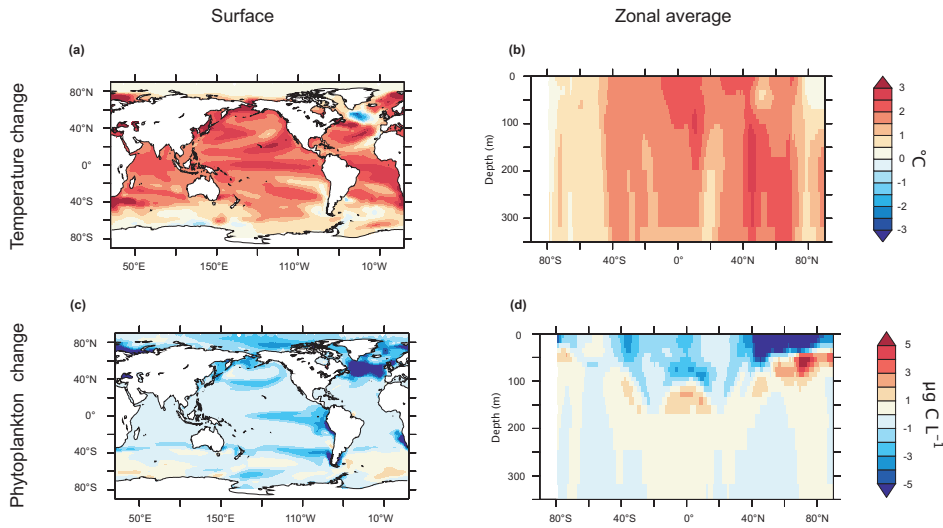
**Figure 3**

Zonally averaged changes (i.e. present – future) in the abundance and the relative abundance of each foraminifer species simulated in FORAMCLIM at (a,c) the ocean surface, and (b, d) integrated throughout the water column.



**Figure 4**

Future changes by 2100 in the dominant environmental drivers of foraminiferal abundance. Ocean temperature ( $^{\circ}\text{C}$ ): (a) at the surface and (b) zonally averaged. Phytoplankton concentration ( $\mu\text{C L}^{-1}$ ): (c) at the surface, and (d) zonally averaged.



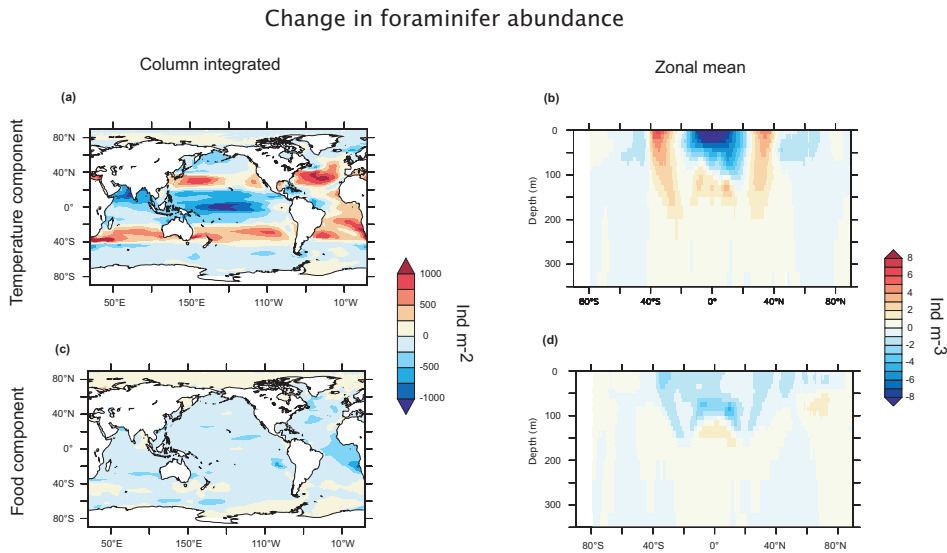
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**Figure 5**

Components of the future change by 2100 in total **foraminiferal** abundance due to temperature: (a) depth integrated ( $\text{Ind m}^{-2}$ ), (b) zonally-averaged ( $\text{Ind m}^{-3}$ ). Components of the future change in total **foraminiferal** abundance due to food availability: (c) depth integrated ( $\text{Ind m}^{-2}$ ), (d) zonally-averaged ( $\text{Ind m}^{-3}$ ).

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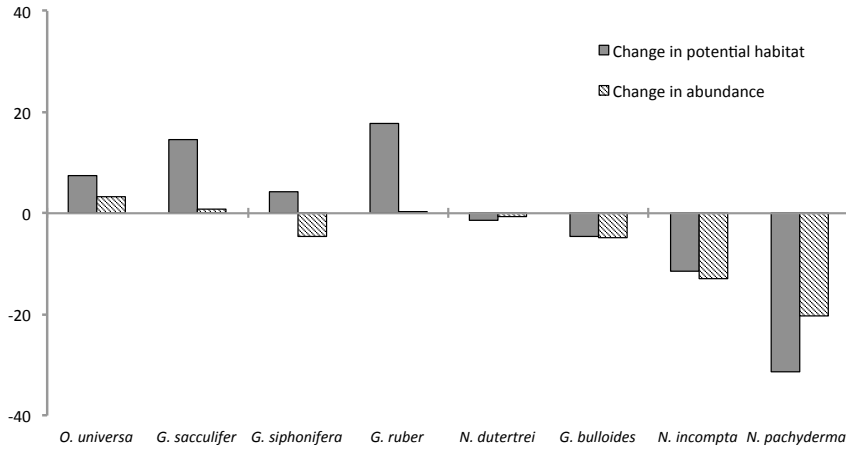
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**Figure 6**

Future change (%) in the potential habitat range (blue) and abundance (red) of each foraminiferal species. Potential habitat range is defined as the area where a foraminifer has the potential to grow given the environmental conditions (i.e. temperature, food availability and light).

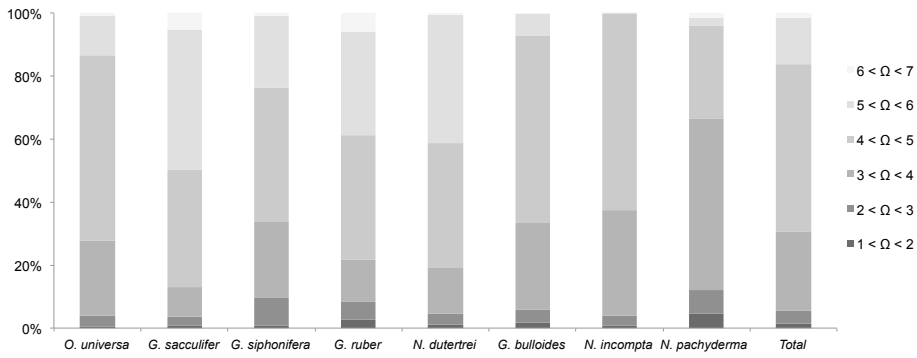


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**Figure 7**

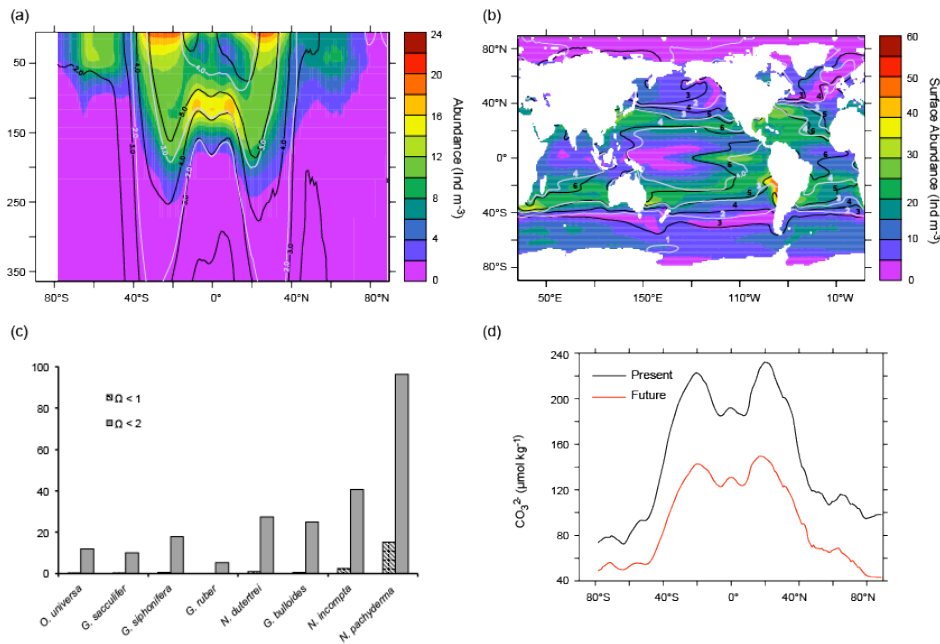
Percentage of the foraminiferal species abundance, collected with multinet plankton tows, that resides in each  $\Omega_c$  class.

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**Figure 8**

Future changes in carbon chemistry of the potential suitable habitat of foraminifera. Simulated present-day total abundance of foraminifera: (a) zonal mean ( $\text{Ind m}^{-3}$ ), and (b) surface ( $\text{Ind m}^{-3}$ ). Contours represent the calcite saturation state,  $\Omega_C$ , for the present-day (black) and the future (pale blue). For each foraminifer species: (c) the percentage of the future potential habitat with low calcite saturation states,  $\Omega_C < 2$ , and (d) the simulated present and future carbonate ion concentration ( $\mu\text{mol kg}^{-1}$ ) of the potential habitat.



## 8. Supplementary material

**Figure S1**

Temperature dependence of the nutrition component of the growth rate ( $\text{day}^{-1}$ , see  $N(T,F)$  in Lombard *et al.*, 2009a) for the eight species included in the FORAMCLIM model.

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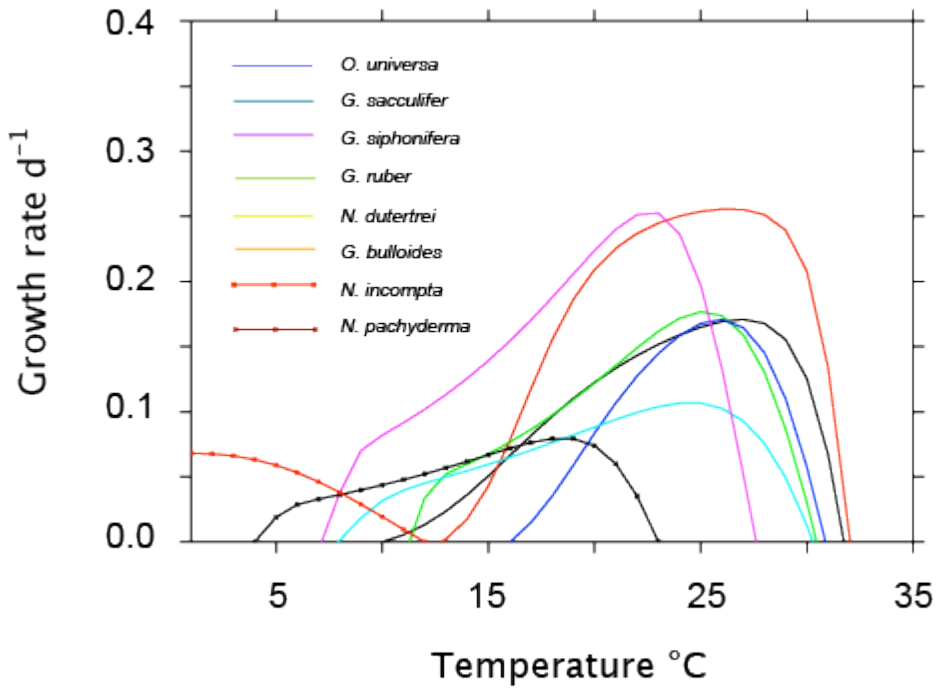
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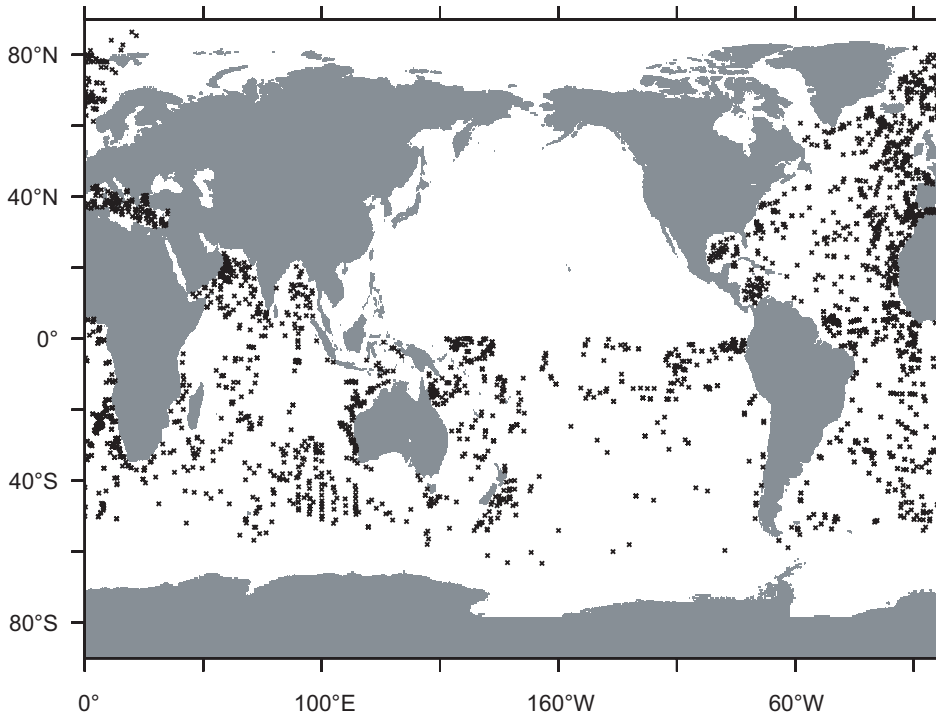


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**Figure S2**

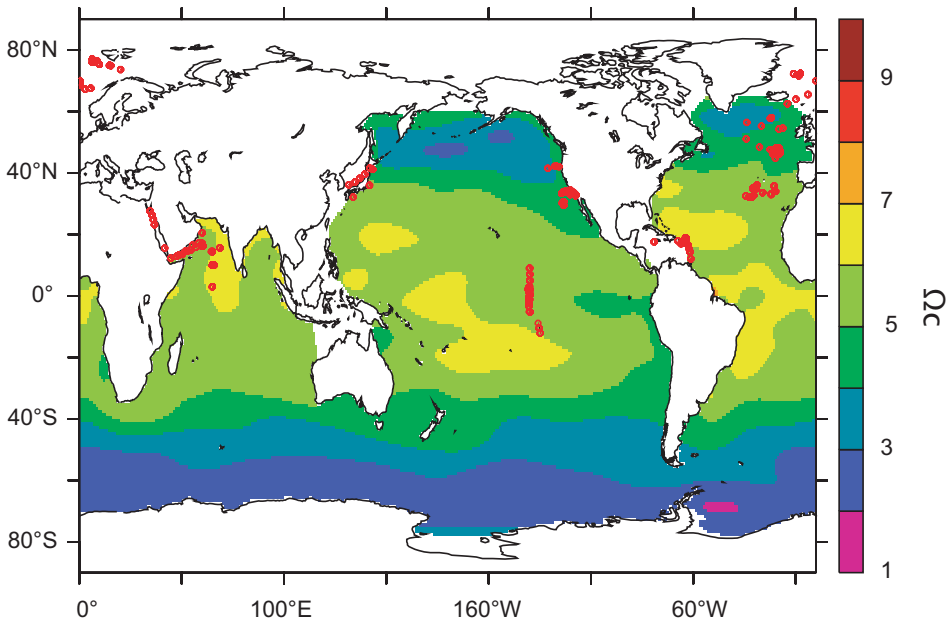
(a) Locations of top-core sediment core data (MARGO database) used for model evaluation. (b) The calcite saturation state of the surface ocean from GLODAP (Key *et al.*, 2004). Red crosses are the locations of multinet plankton tows used to 'sample' the calcite saturation state of present-day foraminiferal habitat (Field, 2004; Kuroyanagi and Kawahata, 2004; Schiebel *et al.*, 2001, 2004; Watkins *et al.*, 1996, 1998).

(a)



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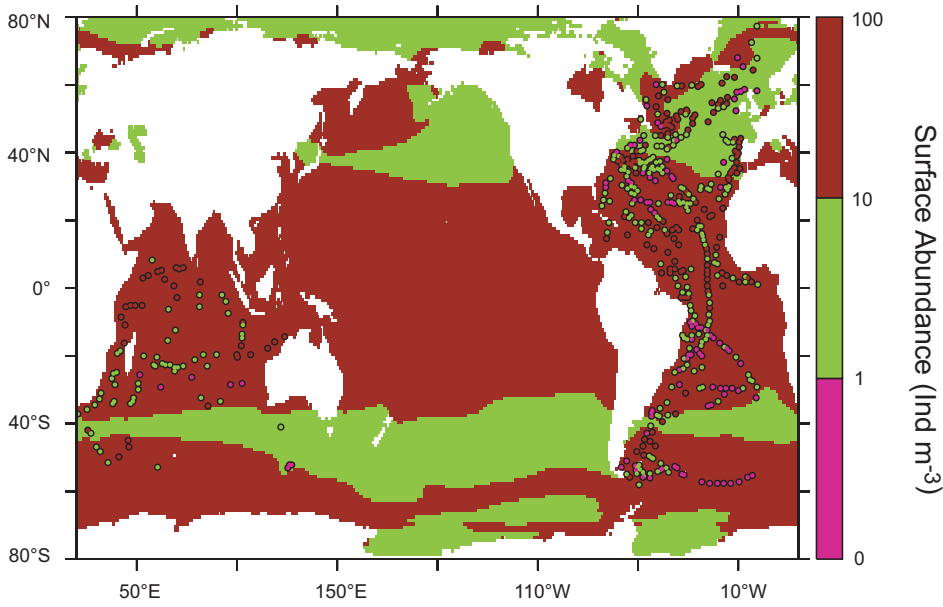
(b)



**Figure S3**

Present-day (simulated and observed) surface (a) total (all species) **foraminiferal** abundance ( $\text{Ind m}^{-3}$ ), and (b) dominant **foraminiferal** species (i.e. the most abundant) based on the eight species included in the FORAMCLIM model. Circles represent the surface plankton tow data of Bé and Tolderlund (1971).

(a)



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(b)

