# Marine zooplankton acclimated to geological warming but face limits by the next century

Rui Ying, Fanny M. Monteiro, Jamie D. Wilson, Daniela N. Schmidt

1 School of Earth Sciences, University of Bristol, Bristol, UK
2 School of Geographical Sciences, University of Bristol, Bristol, UK
3 Department of Earth, Ocean and Ecological Sciences, University of Liverpool, Liverpool, UK

*Correspondence: rui.ying@bristol.ac.uk

## Abstract

Climate changes have threatened marine organisms causing migrations, biomass reduction and extinctions. However, the capacity of marine species to adapt or acclimate to these changes remains poorly constrained in both geological and anthropogenic timescales. Such uncertainty makes modelling past and future ocean biodiversity and ecosystem functions challenging, particularly for the plankton community transferring energy to the whole ocean food web. Here, we use both fossil record observations and a global trait-based plankton model to show that spinose (symbiont and non-symbiont) foraminifera ecogroups acclimated to the slow deglacial transition from the Last Glacial Maximum (LGM, 21 ka) to the pre-industrial period. Non-spinose (non-symbiont) foraminifera kept the same thermal preference. Our study thus provides the first evidence that marine plankton can acclimate during the last deglacial warming, which we confirm by re-analyzing a longer-term global fossil observation (600 ka). However, when forcing the trait-based plankton model with rapid transient warming to next century, our model suggests that the acclimation capacity of these ecogroups is saturating. Foraminifera are projected to migrate poleward, dropping their global biomass by 2.5-12.2% by 2100 relative to 2022 (depending on the warming scenarios). Our study highlights the impact of warming timescale on determining plankton acclimation and migration. Anthropogenic warming is modifying the long-term acclimation pattern of marine zooplankton and causing species distributional change, biodiversity loss, and decreasing fishery production, which could worsen considering the effects of ocean acidification and symbiont bleaching.

## Main text

Geological and modern climate changes have threatened marine biodiversity and ecosystem function (*1*, *2*). To avoid extinction, marine taxa have shifted their habitat to more suitable environments (*3*–*6*). Alternatively, some species can persist in the local environment by adjusting their physiology, which are called adaptation (i.e., evolution) or acclimation (i.e., phenotypic plasticity). These processes are particularly observed in marine microbes (plankton) (*7*–*10*) that have remarkable abundance and short reproductive cycles. However, the capacity of plankton species to adapt and acclimate remains poorly constrained in both past and ongoing climate events. Lack of this knowledge causes uncertainty in estimating plankton extinction risk (*11*), distributional shifts (*12*, *13*), and energy supply to the whole marine food web (*14*) in the warming future.

Understanding adaptation and acclimation in geological time also informs marine faunal-based paleoclimatology reconstructions. Prior studies have used calcifying plankton to estimate past ocean temperatures relying on the idea that fossil assemblages have the same thermal preference as modern assemblages ("transfer function" proxies) (*15*, *16*). For instance, planktic foraminifera are one of the most studied marine calcifying zooplankton in the paleoceanography proxies and contribute to roughly half of the modern ocean calcium carbonate production (*17*). Their ecological niche was suggested to be conservative (i.e., no acclimation) during glacial-interglacial cycles (*18*, *19*). However, this appears to contrast with their observed extensive phenotypic plasticity in both modern (*20*, *21*) and past (*22*), particularly for some warm-water species (*19*). A further examination of foraminiferal acclimation ability is required to improve our understanding of past sea surface temperature.

Here we modeled the thermal performance of planktic foraminifera community in the geological, modern, and future climates. We applied an Earth System Model of Intermediate Complexity (cGENIE) to (a) the Last Glacial Maximum (LGM; ~21,000 years ago, ~6°C cooler than pre-industrial era, Fig. S1); (b) the pre-industrial (PI, 1765-1850), era; (c) and the next century (2100) under 1-4 °C warming scenarios relative to the pre-industrial age. The cGENIE Earth System Model includes a trait-based mechanistic plankton model (*23*) that incorporates the main foraminifera ecogroups distinguished by presence/absence of photosynthetic symbionts and presence/absence of calcareous spines associated with grazing enhancement (*24*). Each ecogroup's thermal performance is flexible and depends on the interaction between the ecogoup’s set of functional traits (size, spine, symbiont) and abiotic (temperature, nutrient, light) and biotic environmental conditions (resource competition and grazing pressure from higher trophic levels) (see **Materials and Methods**). We also estimated the observed foraminifera thermal performance in the LGM and PI using fossil records of foraminifera shells and related geochemical temperature reconstruction (see **Materials and Methods**).

## Plankton thermal performance changes during the last deglacial warming

Our model and fossil observation show that two out of three foraminifera ecogroups acclimated to warmer temperatures during the last deglacial period. The symbiont-barren non-spinose foraminifera keep a preference to grow in cold waters at around –1 to 0°C during the warming (Fig. 1). This conservative thermal preference accompanies their notable poleward displacement toward the Arctic (Fig. S2). In contrast, the other two spinose ecogroups display a strong thermal acclimating capacity, adjusting their niche to grow in warmer waters (Fig. 1). Symbiont-barren spinose foraminifera increased their thermal optimum by about 7°C (from 5°C to 10/13 °C in the observations/model; Fig. 1) allowing them to stay in the subpolar/temperate regions (Fig. S2). Symbiont-obligate spinose foraminifera show the highest acclimation capacity, increasing their thermal optimum by about 10°C (from 19/21°C to 30/29°C in the model/observations; Fig. 1) allowing them to stay in the low latitudes (Fig. S2). These results agree with previous studies that warm-water species' optimal niche (i.e., a subset of niche where they exhibit the highest fitness) has greater variability (*19*).

This ecogroup acclimation could come from species compositional turnover or predominantly represent those abundant species (*Neogloboquadrina pachyderma, Globigerina bulloides, Globigerinoides ruber albus*; Table S1). To test this, we estimated the thermal performance of the top 26 foraminifera species from the fossil observations (Fig. S3). We found that most species increased their thermal optimum, therefore suggesting that the ecogroup response is widespread and not the result of compositional change (Fig. S3-4). However, species acclimated to a different degree, and the difference of species optimal temperature change cannot be explained by symbiont (two-way ANOVA test, $F_{1,26} = 0.434$, $p = 0.516$) or spine trait only (two-way ANOVA test, $F_{1,26} = 1.675$, $p = 0.207$). For example, symbiont-barren non-spinose *Turborotalita quinqueloba* exhibited a 6°C shift, while *Neogloboquadrina pachyderma* and *Neogloboquadrina incompta* in the same ecogroup exhibited a 2 °C change. Symbiont-bearing *Globigerinoides ruber albus* and *Globoturborotalita rubescens* display the largest species-specific thermal optimum change (8 and 9 °C), while *Globigerinoides ruber ruber* only shows 4 °C change. Such result indicates species response are more diverse than the ecogroup model, which misses other important functional traits or trait variations.

## Plankton thermal performance and geographical distribution in the future

Given the thermal acclimation identified in deglacial warmings, the question arising is whether this process protects foraminifera from the threat of rapid anthropogenic warming. To answer this question, we conducted a series of transient simulations from a pre-industrial climate to 2100 forced with idealized anthropogenic $CO_2$ scenarios, using the same model for the last deglacial warming experiment (see **Materials and Methods**). We investigated the marine ecosystem response to four warming scenarios (+1.5, 2, 3, and 4°C by 2100 relative to the 1900-1950 average; Fig. 2 and S5). The model and observation agree that the global mean sea-surface temperature (SST) in the present-day (2022) is already ~0.5 °C warmer than in 1975 (Fig 2a). By 2100, such differences will enlarge to 0.9, 1.1, 1.9, and 2.7°C under the respective four scenarios. In response to these warmings, the ocean net primary production (NPP) drops by 3.9, 5.2, 8.9, and 12.8%, respectively (Fig. 2a). Our model responses are within the Coupled Model Intercomparison Project (CMIP5-6) range (Fig S5-6).

Unexpectedly, the modeled future foraminifera do not acclimate as much as in the deglacial warming (Fig. 2) despite experiencing a lower warming (1-4 °C compared to 6 °C). Planktic foraminifera thus will be driven to migrate poleward by 2100, as the observation since the pre-industrial period (*27*). Specifically, our model predicts that warm-adapted taxa (symbiont-obligate spinose) will increase biomass in the colder waters of the subantarctic zone and the North subpolar regions (Fig. 2c). The changes have already been observed in the Arctic (*28*) and cold upwelling area of the Santa Barbara Basin (*29*). Our model also predicts symbiont-barren spinose foraminifera, such as *G. bulloides*, to increase biomass in the Southern Ocean and North Atlantic (Fig. 2c). This invasion could induce new competition with local symbiont-barren non-spinoses, such as *N. pachyderma* (*30*), that has the unique ability to overwinter in sea ice (*31*).

Along with poleward migrations, the future limited thermal acclimation of foraminifera causes a global biomass reduction (Fig 2a). The model estimates that global foraminifera biomass has declined by 2.3% in the present-year (2022) relative to 1975 (Fig 2a). With a warming of 1.5, 2, 3, and 4°C by 2100, foraminifera biomass reduces further to 4.8, 6.4, 9.8% and 14.3%, respectively. This biomass loss is widespread across the ocean except in the Southern Ocean and to a lower degree in the North subpolar regions, where migration occurs (Fig. 2c). This biomass loss is uneven across ecogroups. It is primarily driven by the two symbiont-barren groups (8-24% and 8-22% for spinose and non-spinose, respectively) accounting for ~75% of the total foraminifera biomass change (between 1975 and 2100; Fig. S7). These non-symbiont groups are the most impacted probably because they are heterotrophic feeders, which rely for food only on a decreasing phytoplankton biomass. In contrast, symbiotic foraminifera are more resilient (1-10% biomass loss; Fig. S7) relying on multiple energy pathways and already adapted to a warm environment. This impact could be even more pronounced when considering the potential effect of ocean acidification on calcification (*32*, *33*) and symbiont bleaching , which is not included in our model.

## Discussion

In contrast to previous studies suggesting conservative planktic foraminifera niche (*18*, *19*, *34*), our results reveal that that foraminifera can shift thermal niche and acclimate to geological warming. We argue that previous studies focusing on the overall niche similarity (*18*, *19*) and occurrence data masked the change of thermal maximum or optimum (*7*, *8*). Both Antell et al. (2021) and Waterson et al. (2016) used probability density function to reconstruct foraminifera niche in the glacial-interglacial cycle and calculated the niche similarity (overlapping). Antell et al. (2021) found that the niche dissimilarity every adjacent 8 ka was not significantly correlated with the change of annual mean ocean temperature (mostly < 1 °C). However, by reanalyzing the species optimal temperature in Antell et al. (*18*), we find opposingly significant relationship ($p = 0.0086$; Fig. 3b), suggesting that foraminifera (24 species) have generally acclimated their thermal optimums in the past 600 ka. Meanwhile, species optimal temperature shows more plasticity than overall niche dissimilarities. The reanalyzed optimal temperature ranges from -5 to +5 °C (Fig. 3b), while the original niche dissimilarities were less than 20% (*18*). In fact, using an idealized well-sampled SST normal distribution ($n=1000$), we find even lower dissimilarity (5%) under a 1 °C shift (Fig. 3a). Therefore, we conclude that overall niche dissimilarity masks the acclimation response of foraminifera to glacial-interglacial climatic variability, and our finding in the LGM and PI is replicated in the longer geological time.

The shifted thermal preference align well with foraminifera's strong morphological and physiological plasticity (*20*, *21*). It could be associated with the foraminifera evolution which also occurred in the late Quaternary glacial-interglacial cycles (*35*). Thermal acclimation capacity of foraminifera allows them to persist in a dynamic climate and increase their successful species evolution given sufficient time. However, the acclimation brings uncertainties of several fixed niche-based approaches. The modern assemblage of foraminifera has been used to reconstruct glacial surface ocean temperature (*36*). But our results show that their LGM assemblage are more cold acclimated (Fig. 1), which indicates that the glacial sea surface temperatures are overestimated using transfer function particularly in the subtropical and tropical regions (*37*). Similar logics applies to the numerical models with fixed niche. Previous foraminifera model ForamCLIM (*38*) based on experimental growth curves projected more foraminifera in subtropics and less in subpolar with ocean warming. But this contrasts with increasing foraminifera abundance observed in the Southern Ocean since 1997 (*39*) and our model results (Fig. 2).

If our model captures the foraminifera acclimation mechanism correctly as suggested by the comparison with LGM observations, such capacity faces saturation in the future. This disparity might come from the fact that the increasing ocean temperature is approaching the maximum tolerable temperatures of the current foraminifera trait set in the model. Alternatively, it can arise from the difference between the LGM equilibrium experiment and a future abrupt warming where environmental changes are different and still developing. Either is within the paradigm that the interplay between plankton acclimation capacity and climatic risks determines their response to environmental changes. During long-term slow climatic transition, acclimating response of foraminifer are supported (Fig. 1; Fig. 3). But In the abrupt events such as the Heinrich cooling event at 16.8 ka, the onset of Holocene at 11 ka (*40*), the modern warming (*27*), and our future projection (Fig. 2), foraminifera assemblage mostly showed migration instead of acclimation. These observations combined with our model are congruent with adaptation and acclimation mechanism that involve the environmental selection of successful genotypes/phenotypes in offspring populations and are susceptible to the high stress of abrupt change (*41*).

Marine plankton determine the amount of energy and material flux through marine food web and the export of photosynthetically fixed carbon to deep oceans. They have strong adapting and acclimating capacity, which was proposed to mitigate the climate impacts and maintain their current ecosystem functions (*7*–*10*). However, we show that such capacity is species-dependent and its function to avoid extinction also depends on the stress level of climate change. Marine zooplankton like foraminifera with strong resilience in the past are projected to face acclimation limits in the high-emission future, agreeing with other species like copepods (*42*), fishes and crustaceans (*43*). Such vulnerability of marine ecosystem could be greater due to ocean acidification (*32*, *33*), symbiont bleaching (*34*), deoxygenation and potentially synergistic stressors. Some immobile species also face dispersal limits due to the barrier of coastlines and frontal systems (*44*, *45*). In conclusion, human-induced rapid changes are breaking the long-term acclimation pattern of marine plankton and threatening the marine biodiversity and ecosystem function. Mitigation policies to prevent the accelerating climate changes are urgently needed to conserve the marine ecosystem.

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## Figures

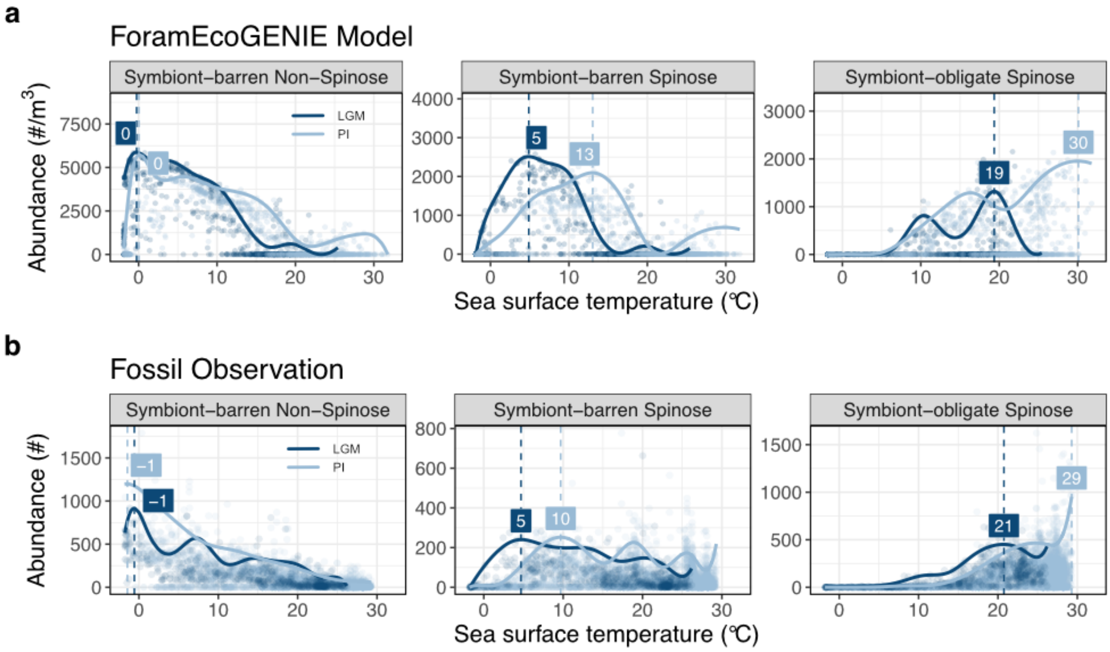

**Fig. 1. Reconstructed thermal performance of planktic foraminiferal ecogroups during the Last Glacial Maximum (dark blue, 18-21 ka) and the pre-industrial age (light blue, 0 ka).** (a) ForamEcoGENIE model output and (b) fossil records. Raw data are plotted in shaded dots. We estimated the maximum thermal performance curves (continuous lines) as an unweighted 95$^{th}$ quantile regression following Kremer et al. (2017; (*45*). We plotted the optimal temperature (vertical dashed lines) as the best temperature for species performance (abundance). The change of optimal temperature shows foraminifer acclimation potential to the deglacial warming. In this figure, we do not represent symbiont-facultative species whose symbiosis mechanism is still ambiguous, although these species can still show thermal acclimation as in the Fig S4. Also note the symbiont-barren spinose ecogroup has more than one optimal temperature which is not labeled.

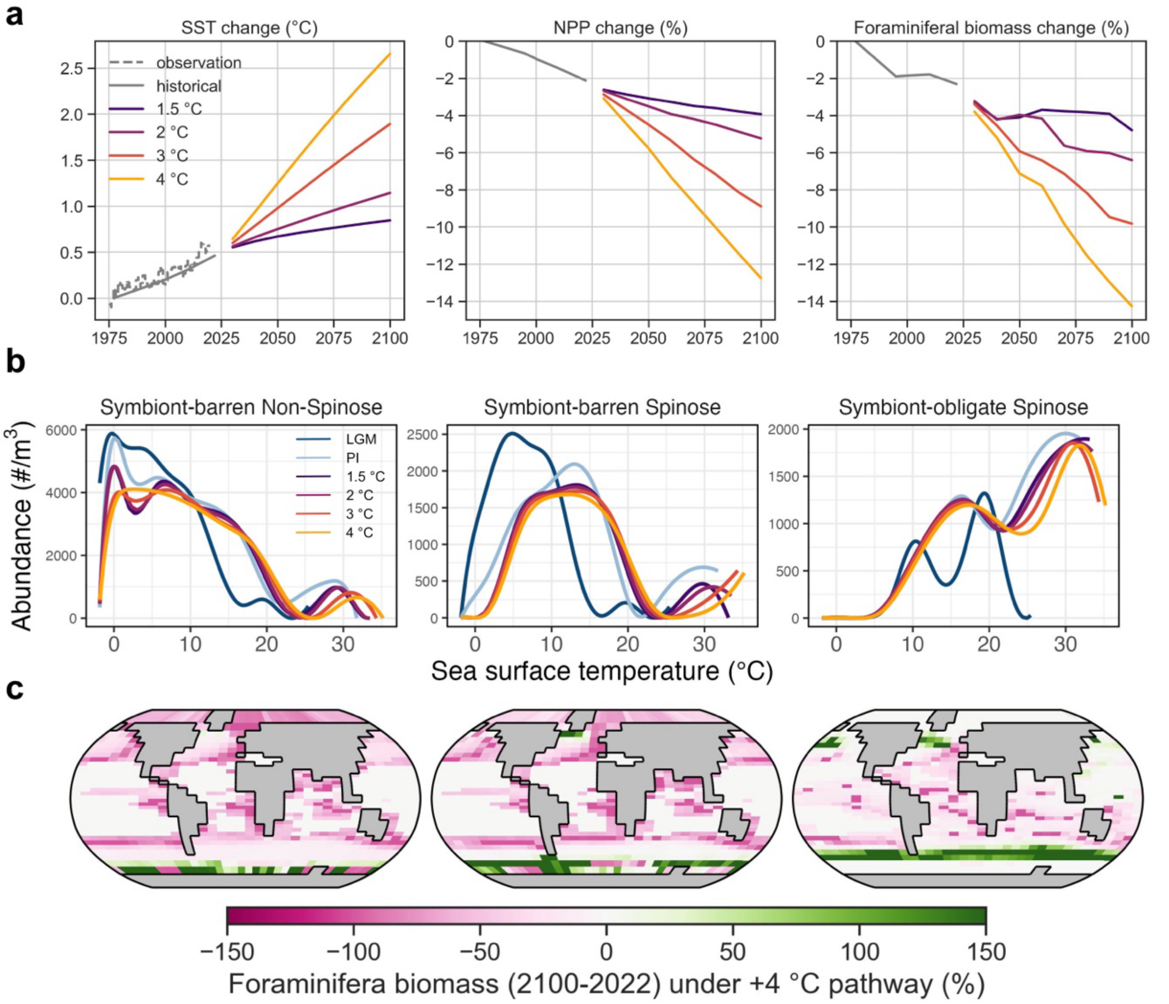

**Fig. 2. Plankton ecosystem response to future anthropogenic warming in cGENIE.**
(a) Modeled change in sea-surface temperature, net primary production, and globally integrated foraminifera biomass when global mean surface temperature increases by 1.5, 2, 3, and 4°C by 2100 relative to the 1900-1950 average. The historical observation of SST is from ERSSTv5 (*18*). We used linear $CO_2$ forcings to mimic global warming. (b) Thermal performance curves of the three foraminifera ecogroups as estimated in Fig. 1 and compared to LGM and PI trends. Only the symbiont-obligate foraminifera experiences slight acclimation at 20-30 °C. (c) Biomass change of each foraminifera group under +4 °C scenario by 2100 relative to the present year (2022).

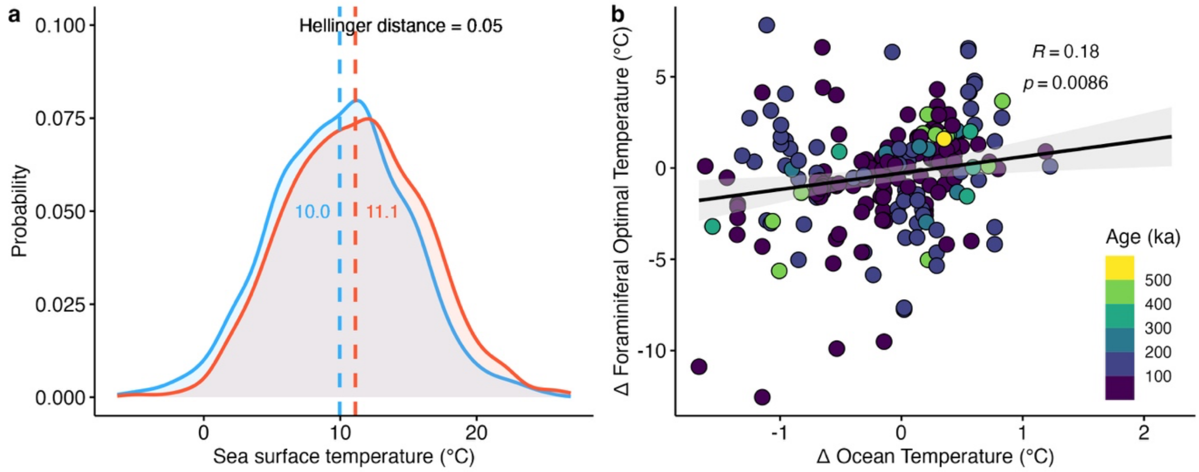

**Fig. 3. Foraminiferal thermal acclimation in longer glacial-interglacial cycles (0-600 ka).** (a) A schematic example of a normal distribution with mean value of 10 and 11 °C (vertical lines, with standard deviation of 5 °C), which shows the high similarity measured in Hellinger's distance (value range from 0 to 1, where a lower value is more similar) used in Antell et al. (*18*) that reconstructed thermal niches change using Kernel Density Estimate (KDE) probability density distribution. (b) Based on the same data, we calculate the changes of each species' (n=24) optimal temperature (with the probability peaks) and corresponding regional mean temperature change every 8 ka. We filter the samples with an insufficient number of occurrences (n=20) to achieve a robust reconstruction. The weak but significant relationship (p=0.0086, R=0.18) between ocean temperature change and species optimal temperature change indicates consistent thermal acclimation in the past 600 ka, while the rest of variance can come from uncounted climatic drivers and species-specific difference as the LGM/PI.