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# Exploring the impact of climate change on the global distribution of non-spinose planktonic foraminifera using a trait-based ecosystem model

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## Abstract

Planktonic foraminifera are one of the primary calcifiers in the modern ocean, contributing 23%–56% of total global pelagic carbonate production. However, a mechanistic understanding of how physiology and environmental conditions control their abundance and distribution is lacking, hindering the projection of the impact of future climate change. This understanding is important, not only for ecosystem dynamics, but also for marine carbon cycling because of foraminifera's key role in carbonate production. Here we present and apply a global trait-based ecosystem model of non-spinose planktonic foraminifera ('ForamEcoGENIE') to assess their ecology and global distribution under future climate change. ForamEcoGENIE considers the traits of calcium carbonate production, shell size, and foraging. It captures the main characteristic of biogeographical patterns of non-spinose species – with maximum biomass concentrations found in mid- to high-latitude waters and upwelling areas. The model also reproduces the magnitude of global carbonate production relatively well, although the foraminifera standing stock is systematically overestimated. In response to future scenarios of rising atmospheric CO<sub>2</sub> (RCP6 and RCP8.5), on a regional scale, the modelled foraminifera biomass and export flux increases in the subpolar regions of the North Atlantic and the Southern Ocean while it decreases everywhere else. In the absence of adaptation, the biomass decline in the low-latitude South Pacific suggests extirpation. The model projects a global average loss in non-spinose foraminifera biomass between 8% (RCP6) and 11% (RCP8.5) by 2050 and between 14% and 18% by 2100 as a response to ocean warming and associated changes in primary production and ecological dynamics. Global calcium carbonate flux associated with non-spinose foraminifera declines by 13%–18% by 2100. That decline can slow down the ocean carbonate pump and create short-term positive feedback on rising atmospheric pCO<sub>2</sub>.

## KEYWORDS

calcium carbonate export, plankton ecology, planktonic foraminifera, trait-based model

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## 1 | INTRODUCTION

Planktonic foraminifera are calcifying marine protists. They occupy habitats generally at the top 100 m of the ocean (Berger, 1969; Field, 2004; Schiebel et al., 2001), although some species are found in sub-thermocline waters (200–2000 m, Schiebel & Hemleben, 2005). Planktonic foraminifera are one of the least abundant zooplankton groups in the ocean, contributing less than 5% to the total microzooplankton abundance (Beers & Stewart, 1971) and 0.04% of the total plankton biomass in the upper 200 m (Buitenhuis et al., 2013). Despite this, planktonic foraminifera play a major role in the calcium carbonate ( $\text{CaCO}_3$ ) budget of the ocean and are thought to be responsible for 23%–56% of pelagic  $\text{CaCO}_3$  flux globally (Buitenhuis et al., 2019; Schiebel, 2002).

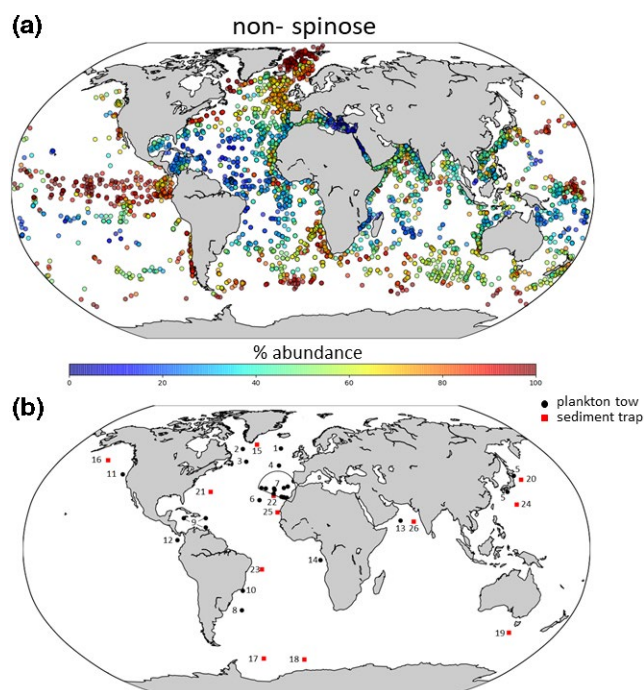
$\text{CaCO}_3$  shells precipitated by foraminifera in the surface ocean ultimately sink through the water column. Some dissolve along the way and others at the sediment surface of the deep ocean. The associated removal of alkalinity and dissolved inorganic carbon (DIC) from surface seawater lowers pH. This favours dissolved carbon as  $\text{CO}_{2(\text{aq})}$  over carbonate ions ( $\text{CO}_3^{2-}$ ), and on anthropogenic timescales (c.  $<10^3$  years), increases  $\text{CO}_2$  in the atmosphere (Frankignoulle et al., 1994). Any reduction in the rate of biogenic carbonate precipitation at the ocean surface would therefore have a (short term) positive impact on atmospheric  $\text{CO}_2$ . On longer timescales (order  $10^3$ – $10^4$  years), lower pelagic  $\text{CaCO}_3$  production and removal through burial in the sediments would act to increase  $\text{CO}_3^{2-}$  concentrations and hence lower atmospheric  $\text{CO}_2$  (Ridgwell & Zeebe, 2005). Following burial in sediments, the carbonate shells of planktonic foraminifera also provide essential proxy records, widely used to reconstruct past environmental conditions in the ocean, such as temperature, salinity, circulation, oxygenation, and alkalinity (Henderson, 2002 and references within).

Despite planktonic foraminifera's importance to the marine carbon cycle, little is known about how their distribution and biomass may be impacted by climate change, and the strength and sign of the feedback with atmospheric  $\text{CO}_2$  is uncertain (Ridgwell et al., 2009). This lack of understanding is partly a consequence of the difficulty of sampling low standing stocks as well as due to a generally unsuccessful reproductive cycle in culture (Schiebel & Hemleben, 2017). Temperature has previously been suggested to be the main abiotic driver of foraminifera biogeography (CLIMAP, 1976), followed by other environmental factors such as light attenuation, stratification, and carbonate saturation (Bé & Tolderlund, 1971; Ottens & Nederbragt, 1992; Schiebel et al., 2001; Schmidt, Renaud, et al., 2004; Storz et al., 2009). Warming since the 1970s has led to changes in their distribution as recorded in sediment traps and plankton tows (Beaugrand et al., 2012; Jonkers et al., 2019). Latitudinal shifts of assemblages by 40 km per decade have led to habitat expansion of warm-adapted species (Beaugrand et al., 2012; Field et al., 2006; Jonkers et al., 2019).

Prey availability has also been considered a key driver of planktonic foraminifera biogeography (Schiebel & Hemleben, 2017), although understanding of predator–prey interactions is equally

limited. Planktonic foraminifera are immotile passive ambush feeders (Kjørboe, 2011), that use their rhizopodia's nets to sense, encounter, and control prey from their surroundings (e.g. Anderson & Be, 1976). Field observations and culture experiments suggest that foraminifera are opportunistic omnivorous predators, with feeding preferences being linked to their external morphology (e.g. Anderson & Be, 1976; Anderson et al., 1979; Spindler et al., 1984). Roughly, half of foraminifera species develop calcium carbonate spines during their juvenile stages (called spinose). Spinose adult species (with the exception of *Globigerina bulloides*) are predominantly carnivorous and most abundant in oligotrophic regions (Schiebel & Hemleben, 2017). In contrast, adults of non-spinose species are mostly herbivorous and potentially supplement their diet with organic matter and animal prey (dead or alive, Anderson et al., 1979; Greco et al., 2021; Schiebel & Hemleben, 2017). Non-spinose species are most abundant in highly productive areas (Figure 1a; Bé & Tolderlund, 1971).

In addition to controlling species biogeography, environmental conditions also impact the growth and calcification rates of individuals (e.g. Anderson et al., 1979; Davis et al., 2013; Schmidt, Renaud, et al., 2004; Weinkauff & Waniek, 2016). For example, starvation causes shell size reduction and death, while over-feeding leads to a shell size increase and a shorter lifespan (e.g. Anderson et al., 1979; Bé et al., 1981; Caron & Bé, 1984). Shell size is also correlated with temperature, with a large size under optimal conditions (Hecht, 1976; Schmidt, Thierstein, et al., 2004). In contrast, our understanding of



**FIGURE 1** (a) Contribution of non-spinose foraminifera to foraminifera assemblages based on sediment traps (ForCenS database; Siccha & Kucera, 2017). Data meta-analysis by Kirsty Edgar. (b) Locations of the plankton net (circle) and sediment trap (square) observations of non-spinose species were used for the model-data comparison. The references are listed in Tables S1 and S2

processes that drive shell density and weight and hence 'calcification' in general, is less clearly developed; species can grow in shell size but develop thinner shells and vice versa. For example, while some studies suggest that pCO<sub>2</sub> regulates calcification and shell morphology (e.g. Barker & Elderfield, 2002; Bijma et al., 1999; De Moel et al., 2009; Lombard et al., 2010; Moy et al., 2009; Russell et al., 2004; Spero et al., 1997), others suggest a combination of multiple environmental drivers (Davis et al., 2013; Weinkauff & Waniek, 2016; Zarkogiannis et al., 2019 and references within; Fox et al., 2020). Jointly, these studies indicate species-specific regional responses (e.g. Barker & Elderfield, 2002; Davis et al., 2013; Fox et al., 2020; Weinkauff & Waniek, 2016).

As a result of all these uncertainties surrounding the influences of various environmental drivers on planktonic foraminifera, it is difficult to quantify the impact of future climate change, particularly in terms of their biogeography, regional extirpation, biomass, and consequently calcium carbonate production. To better understand how climate influences future foraminifera distribution and biomass, we require a mechanistic way of connecting their physiology with the environment. A promising mechanistic approach for studying complex ecosystem behaviour is trait theory, that describes ecosystem dynamics based on individuals' key traits (e.g. size, feeding, motility, reproduction) and trade-offs (e.g. energetic cost, protection benefit; Flynn et al., 2015; Kiørboe et al., 2018b). Trait theory has been used to study the links between environmental conditions and plankton physiology, ecology, and populations, under both modern and future climate conditions (e.g. Brun et al., 2019; Dutkiewicz et al., 2013, 2020; Follows et al., 2007; Ward et al., 2012). Trait-based models also provide a framework for testing environmental impacts on species (such as foraminifera) where physiological information is limited, by exploiting knowledge from different organisms with similar traits. In an initial investigation of applying this approach to foraminifera, Grigoratou et al. (2019) and Grigoratou, Monteiro, Ridgwell, et al. (2021) developed a trait-based model and explored the influence of size, calcification, foraging, diet, and community interactions in planktonic foraminifera in a 0D chemostat setup. Their work suggested that resource competition has a strong effect on non-spinose distribution and indicated that foraminifera's low standing biomass, combined with the carbonate shell, provide protection against predation, pathogen invasion, or/and parasites.

In the present study, we embedded Grigoratou et al.'s (2019; hereafter Grigoratou2019) trait-based model in the 3D ocean circulation component of an Earth System model. This new coupled model – 'ForamEcoGENIE' – is the first global trait-based ecosystem model for planktonic foraminifera and allows us to investigate their distribution based on the traits of carbonate production, shell size, and foraging, as well as to study foraminifera's interactions with other plankton groups. Specifically, we use ForamEcoGENIE here to explore the influence of future warming on the distribution, biomass, and export flux of calcium carbonate from the ocean surface. We focus on symbiont-barren non-spinose foraminifera as this reduces the number of different traits (and associated uncertain trade-offs) that must be accounted for in the model (e.g. spines, symbiosis).

## 2 | METHODS

### 2.1 | Model structure

ForamEcoGENIE comprises an 'Earth System Model of Intermediate Complexity' ('GENIE') coupled with an allometric trait-based plankton community model, the latter being based on the EcoGENIE ecosystem model of Ward et al. (2018) and Grigoratou's (2019) 0D trait-based foraminifera model. A description of ForamEcoGENIE, with an emphasis on the governing equations of foraminifera, is shown in Data S1. The ForamEcoGENIE ocean is implemented on an equal-area 36 × 36 horizontal grid with a uniform resolution in longitude (10° resolution) and increasing resolution in latitude (3.2° at the equator to 19.2° near the poles). The ocean model has 16 vertical layers with non-uniform depth spacing. Also included is a 2D energy-moisture balance atmosphere module (providing warming response to increasing atmospheric CO<sub>2</sub>) and a 2D dynamic-thermodynamic sea-ice module (providing high latitude feedbacks to climate change; Marsh et al., 2011). Despite the coarse resolution, ForamEcoGENIE can resolve the large-scale properties of ocean circulation and plankton biogeography (Ward et al., 2018). For details on model code availability, see the Code and Data Availability section.

The food web in the model resolves a total of 16 plankton groups, which are split into eight different size classes of phytoplankton (autotrophs) and eight different size classes of zooplankton (heterotrophs). One of the 8 heterotroph size classes is reassigned to represent a calcifying zooplankton – here, non-spinose foraminifera (Table 1). In essence, the 0D model from Grigoratou (2019) is replicated across the model surface grid, which is now dynamically interlinked by the modelled climate, circulation, and biogeochemistry. Phytoplankton are limited by light and nutrients (phosphorus, iron) while zooplankton growth depends on prey density and size (Ward et al., 2018). Zooplankton (excluding non-spinose foraminifera) are assumed to be omnivorous active predators. The grazing function of zooplankton follows a Holling type II response with a prey refuge term. The total zooplankton biomass varies as a function of grazing gains, predation, and mortality. Temperature effect on plankton growth is represented with an Arrhenius type equation (Data S1, equation 1). All groups include a background mortality to represent loss due to viral/bacterial infection or natural death. Life cycles and vertical migration are not considered in the model; the plankton biomass is restricted to the model's surface layer (0–80.8 m depth).

### 2.2 | The symbiont barren non-spinose foraminifera functional type

Non-spinose foraminifera are represented by a spherical equivalent shell diameter of 190 μm (Table 1). This shell diameter (190 μm) characterizes adult stages of non-spinose planktonic foraminifera from all species, considering small species such as *Neogloboquadrina pachyderma*, and *Neogloboquadrina incompta* (Schmidt, Renaud, et al., 2004). We define non-spinose foraminifera in the model as passive

No	Phytoplankton	ESD ( $\mu\text{m}$ )	No.	Zooplankton	ESD ( $\mu\text{m}$ )
1	Picophytoplankton	0.6	9	Picozooplankton	1.9
2	Picophytoplankton	1.9	10	Nanozooplankton	6
3	Nanophytoplankton	6	11	Nanozooplankton	19
4	Nanophytoplankton	19	12	Microzooplankton	60
5	Microphytoplankton	60	13	Microzooplankton	190
6	Microphytoplankton	190	14	Mesozooplankton	600
7	Mesophytoplankton	600	15	Mesozooplankton	1900
8	Mesophytoplankton	1900	16	Plank. foraminifera	190

TABLE 1 Plankton functional groups and sizes in ForamEcoGENIE setup

herbivorous feeders, following the observations showing that due to the lack of spines, non-spinose diet mostly consists of phytoplankton (Schiebel & Hemleben, 2017).

As the environmental factors affecting calcification are complex and incompletely understood, we do not explicitly represent the calcification process in the model. Instead, our approach is to simulate the existence of this trait based on the trade-offs of energetic costs versus predation benefits (Grigoratou et al., 2019, more details in Data S1, section 1.2 'ECOGEM'). Following the 'defence' theory, we account for energy loss to be the main cost of creating a shell (in this case, out of calcium carbonate) and protect the main benefit (Ehrlich & Gaedke, 2018; Harvell, 1990). We optimize the costs and benefits of calcification by adjusting foraminifera's maximum growth, background mortality, and predation rates (eqs. (S2, S8)) based on Grigoratou's (2019) approach (see section 2.3 in Grigoratou et al., 2019 for more details). We ran a sensitivity analysis of 27 simulations (Data S2: Tuning ForamEcoGENIE) and compared the model output with empirical observations of non-spinose species abundances from plankton tows and sediment traps (Figures 1–4, Tables S1 and S2). The model-data comparison revealed a best fit to observations when applying a 10% reduction of foraminifera's growth (calcification cost), a 10% reduction in predation, and a 30% reduction in background mortality (calcification benefits; Figures 2a, 3 and 4, Data S2: Tuning ForamEcoGENIE). It should be noted that in optimizing trade-offs, we implicitly consider only the presence/absence of a shell and assumed nothing about the amount of  $\text{CaCO}_3$  that is actually precipitated. Hence, to derive estimates of the calcium carbonate flux associated with foraminifera productivity, we test different assumptions regarding shell weight (the mass of  $\text{CaCO}_3$  per unit mass of foraminifera organic matter) (see 2.3. [Empirical observations of non-spinose foraminifera] for more details).

### 2.3 | Empirical observations of non-spinose foraminifera

For the model-data comparison, we selected empirical observations from plankton tows and sediment traps across 26 representative locations of foraminifera's key geographical zones (Figures 1–4, Tables S1 and S2). We compile observations from sediment traps to investigate the modelled flux. We do not include observations from the

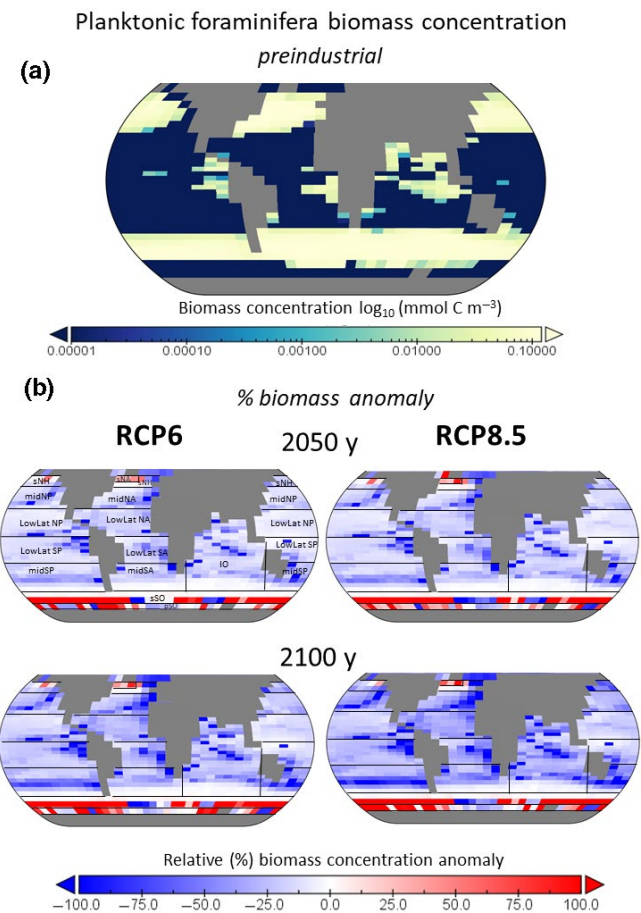
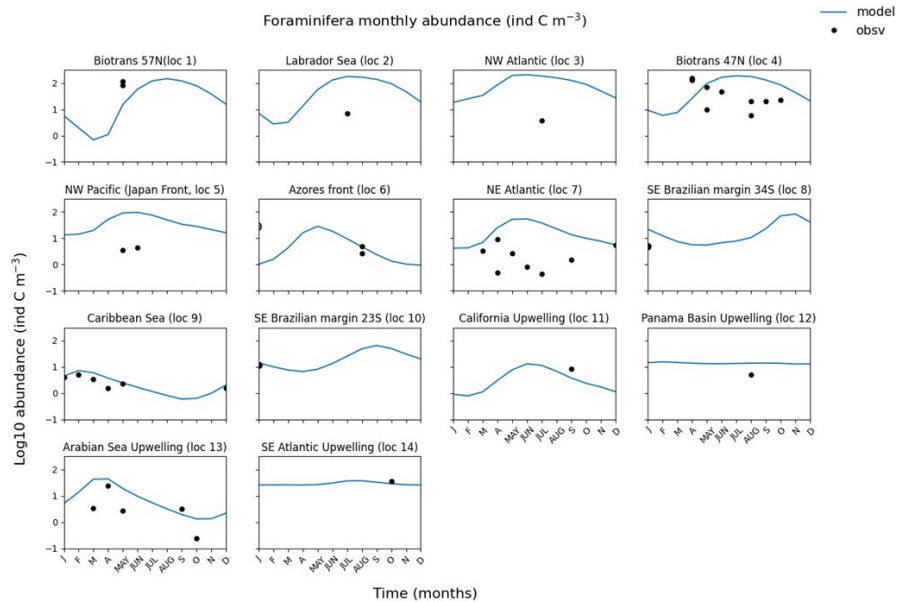


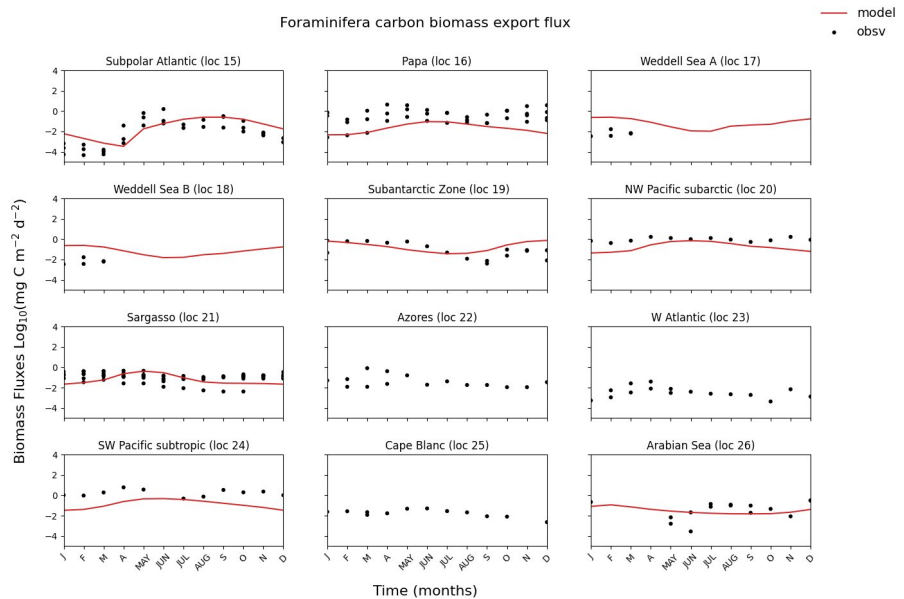
FIGURE 2 (a) Global biomass concentration ( $\log_{10}$  mmol  $\text{C m}^{-3}$ ) of non-spinose planktonic foraminifera in response to pre-industrial  $p\text{CO}_2$  (278 ppm). (b) Relative biomass anomalies (future – pre-industrial) by 2050 and 2100. IO, Indian Ocean; LowLat NA, Low Latitude N. Atlantic; LowLat NP, Low Latitude N. Pacific; LowLat SA, Low Latitude S. Atlantic; LowLat SP, Low Latitude S. Pacific; midNP, mid-latitude N. Pacific; midpNA, mid-latitude N. Atlantic; midSA, mid-latitude S. Atlantic; midSP, mid-latitude S. Pacific; pSO, polar Southern Ocean; sNA, subpolar North Atlantic; sNH, subpolar Northern Hemisphere; sSO, subpolar Southern Ocean. The latitudes and longitudes of the zones can be found in Table S3

Mediterranean Sea and the Arctic Ocean as those regions are poorly spatially resolved in the model and thus excluded from our results. The majority of the plankton tow observations are from the upper

**FIGURE 3** Modelled (blue line) and observed abundance (ind  $m^{-3}$ ) from plankton tows (black dots). The January abundances in the Azores front sample (No. 6) show the winter peak of deep species *G. truncatulinoides*. Locations can be found in Figure 1b and Table S1. Subpolar: loc 1,2, temperate: loc 3–8, (sub)tropical: loc 9, 10, coastal upwelling: 11–14



**FIGURE 4** Modelled (red line) and observed (black dots) foraminifera export flux ( $mg C m^{-2} day^{-1}$ ). Locations are found in Figure 1b and Table S2. In the locations Cape Blanc, Azores, and W Atlantic non-spinose foraminifera are absent in the model; therefore, no model data are shown. Subpolar: loc 15–20, temperate: loc 21, 22, (sub)tropical: loc 23, 24, coastal upwelling: 25, 26



150 m depth (Table S1) where most of the non-spinose species can be found (Bé & Tolderlund, 1971; Berger, 1969; Rebotim et al., 2017).

In the model, foraminifera are simulated in terms of organic biomass concentration ( $mmol C m^{-3}$ ). We also consider the organic matter export flux arising from foraminifera ( $mmol C m^{-3} day^{-1}$ ), which comprises component fluxes from (1) background mortality and (2) the foraminifera biomass which has not been assimilated by predators ('sloppy' feeding; for more details see Ward et al., 2018). To compare with observational abundance data, we converted the modelled foraminifera carbon biomass concentration into abundance using the Schiebel and Movellan's (2012) estimations of the mean organic carbon biomass per individual ( $0.845 \mu g C ind^{-1}$ ). Based on Schiebel and Movellan's (2012) arithmetic mean biomass for the first 80 m and ForamEcoGENIE's sea surface area ( $3.5 \times 10^8 km^2$ , Mediterranean

Sea and Arctic Ocean excluded), we calculate the global foraminifera biomass in the upper 80 m to be equal to 1.5 Tg C. We compare the modelled global biomass with this calculation.

Finally, as ForamEcoGENIE does not explicitly resolve the process of calcification and hence lacks a simulated 'calcium carbonate concentration' equivalent in the ocean surface. We thus estimate the calcium carbonate ( $CaCO_3$ ) export flux directly from the modelled foraminifera organic carbon flux. To do so, we convert the organic carbon export flux into an equivalent of individuals (as before, based on Schiebel & Movellan's, 2012 carbon biomass estimate), and then assume a specific shell weight per individual (in units of  $\mu g CaCO_3 ind^{-1}$ ). Because the shell weights of adult individuals vary significantly across different species and regions (Table S4) – typically from just under  $5 \mu g CaCO_3 ind^{-1}$  (e.g. *Globigerinita glutinata*)

to  $30 \mu\text{g CaCO}_3 \text{ ind}^{-1}$  (e.g. *Globorotalia truncatulinoides*), assuming the arithmetic mean is unlikely to be representative. We hence convert organic carbon flux to that of  $\text{CaCO}_3$  for end-member weights of 5 and  $30 \mu\text{g CaCO}_3 \text{ ind}^{-1}$  to create a maximum range of 'uncertainty'. For simplicity, we also report the results of assuming a typical species shell weight of  $10 \mu\text{g CaCO}_3 \text{ ind}^{-1}$  (Table S4). We compare our global export flux with Schiebel (2002) estimations for the first 100 m.

## 2.4 | Model set up

We spun up the model for 10,000 years under an invariant pre-industrial atmospheric  $\text{CO}_2$  concentration of 278 ppm (as per Ward et al., 2018). The model output from the final year of the spin-up was then used to evaluate the model for pre-industrial climate conditions (hereafter 'pre-industrial'). The spin-up was followed by an experiment run from years 1775 to 2008 with atmospheric composition following observed historical increases, and then from 2008 to 2100 with atmospheric composition following one of two different future  $\text{CO}_2$  scenarios – RCP6 and RCP8.5. In the RCP scenarios, atmospheric  $\text{CO}_2$  at year 2050 reaches 478 ppm (RCP6) or 540 ppm (RCP8.5), and by 2100, 670 ppm (RCP6) or 936 ppm (RCP8.5) (Meinshausen et al., 2011). We present model outputs expressed in terms of biomass concentration anomaly (future industrial and pre-industrial) for 13 geographical zones (Figure 2b, Table S3) and as an annual average of the respective year.

To evaluate the link between foraminifera's distribution and environmental conditions, we applied a pairwise Spearman correlation between foraminifera's biomass, temperature, salinity, nutrient concentration, and with the plankton groups for the following biozones: subpolar, Indian Ocean, mid, and low latitudes. We applied the correlation for the pre-industrial and RCP8.5 scenario (2050, 2100). We ran the statistical analysis in Python 3.9 with the Pingouin0.3.8 software (Vallat, 2018). Further details of the statistical analysis can be found in the Data S1.

## 3 | RESULTS

### 3.1 | Global pre-industrial conditions

#### 3.1.1 | Biogeographical patterns, distribution, and calcium carbonate flux

We start by evaluating ForamEcoGENIE's performance under a pre-industrial climate. The modelled annual mean abundance (biomass concentration converted into a representative number of individuals – see Section 2) of non-spinose foraminifera increases from low latitudes ( $0\text{--}124 \text{ ind m}^{-3}$ ) to coastal upwelling ( $54\text{--}349 \text{ ind m}^{-3}$ ), mid-latitudes ( $357\text{--}612 \text{ ind m}^{-3}$ ) and subpolar ( $518\text{--}538 \text{ ind m}^{-3}$ ) regions. Non-spinose species are absent or in very low abundance in

oligotrophic (sub)tropical regions and the polar waters ( $>66^\circ\text{S}$  lat) of Southern Ocean in the model (Figures 2a, 3 and 4, Data S1). The modelled biogeographical patterns generally agree with the main large-scale features of the relative prevalence of non-spinose species that shows an abundance increase from low to high latitudes (Figures 1a and 2a). For a more in-depth model-data comparison, the reader is referred to Data S1 section 2.1. Comparison with observations.

Considering foraminifera distribution and seasonality, the model overall exhibits a lower variance as compared to field observations and often differs in the timing of the seasonal changes (Figures 3 and 4, Data S1: section 2.1). For instance, although modelled seasonality generally follows the observed patterns in subpolar regions (Figure 4, loc 15–20), it fails to capture the observed seasonal trends in temperate and coastal upwelling systems (Figure 3 (loc 11–14), Figure 4 (loc 21–26)). Modelled flux is within the observed range of sediment trap data for most regions except for three (Azores, W Atlantic, and Cape Blanc) where foraminifera are absent in the model, and the Weddell Sea where the model has higher fluxes (Figure 4, loc 17–18). In contrast, the model overestimates stocks compared to plankton nets in many sampling locations, especially in subpolar and mid-latitude regions (Figure 3, loc 1–8).

Globally, the modelled abundance annual mean of adult non-spinose is  $223 \text{ ind m}^{-3}$ , that equals to a global biomass of 7.5 Tg C. This simulated biomass is higher than the observational-based estimate of 1.5 Tg C, which combines spinose and non-spinose (top 80 m; Schiebel & Movellan, 2012). Based on calculated modelled organic matter export flux from non-spinose foraminifera, we estimate a global foraminifera calcium carbonate flux of between 0.7 and 4.2 Pg  $\text{CaCO}_3$  (for the 5 and  $30 \mu\text{g CaCO}_3$  shell weights, respectively), with an estimate of 1.4 Pg  $\text{CaCO}_3 \text{ year}^{-1}$  assuming a  $10 \mu\text{g CaCO}_3$  shell weight. Previous estimates of foraminifera calcium carbonate flux have an equally large range of 0.4–3.2 Pg  $\text{CaCO}_3 \text{ year}^{-1}$  (Buitenhuis et al., 2019; Schiebel, 2002). We compare our modelled carbonate flux with Schiebel's (2002) estimate as it is the only study that provides global estimates from field data, covering mostly the N. Atlantic and Arabian Sea. This study suggests a 100 m water depth flux of 1.3–3.2 Pg  $\text{CaCO}_3 \text{ year}^{-1}$  for both spinose and non-spinose species. Because non-spinose foraminifera contribute approximately half of global foraminifera assembles (with regional variations), this equates to an observed  $\text{CaCO}_3$  flux from non-spinose foraminifera of 0.7–1.6 Pg  $\text{CaCO}_3 \text{ year}^{-1}$ . Our preferred estimate (1.4 Pg  $\text{CaCO}_3 \text{ year}^{-1}$ ) falls within this range, although our maximum uncertainty estimate (4.2 Pg  $\text{CaCO}_3 \text{ year}^{-1}$ ) is about a factor of 2 higher.

#### 3.1.2 | Model and data limitations

Although our model reproduces the general biogeographical patterns as well as the correct order-of-magnitude of global export flux, the foraminifera biomass standing stock is systematically

overestimated. For many regions, there are also obvious mismatches in the modelled seasonal variation in foraminifera biomass vs. empirical observations. It is difficult to precisely pinpoint the specific causes of this model-data mismatch, but there are four more obvious possibilities that can be explored further in future studies.

1. The seasonal variation mismatches are likely partly a consequence of the relatively low spatial (horizontal and vertical) model resolution which tends to damp climatological seasonality. Moreover, the lack of a coupled dynamical atmosphere (and hence ability to simulate modes of inter-annual variability (such as ENSO) or land surface scheme in ForaminiferaEcoGenIE) will likely smooth out the seasonal signal and induce apparent phase shifts as well as other season cycle distortions. Indeed, while the amplitude of seasonality in Chl *a* and total ecosystem export was shown to be reasonably reproduced in Ward et al. (2018), they noted prominent mismatches in the timing of plankton blooms which will be directly translated into timing issues in foraminifera biomass and fluxes, as seen in the model (Figures 3 and 4).
2. The parameterization of ecological processes in the model may also be contributing to the mismatches. For instance, due to the lack of data on foraminifera calcification trade-offs for growth and protection, in this study we assumed a fixed calcification trade-off and did not consider differencing degrees of calcification and hence trade-off between different species (or as a function of environment).
3. Most of the modelled non-spinose biomass globally comes from the mid-latitudes (Figure 2a) and it is overall higher than the observed. However, *Globigerina bulloides*, an opportunistic herbivorous spinose species, that favours phytoplankton bloom conditions, often dominates the foraminifera assemblages in those regions. The inclusion of *G. bulloides* (a spinose foraminifera) in the model might help competitively reduce our simulated non-spinose population size.
4. Our model-data comparison would benefit from a better data coverage. We compare the model with empirical data collected with plankton nets and sediment traps which provide qualitatively different observations. Traps sample fluxes through the water column for a long time of period. Our monthly flux is within the range to the monthly trap data (Figure 4), giving us some confidence in the model output. In contrast, plankton nets provide snapshots of concentrations of a specific depth and time. Due to the lack of net time-series, the model-data comparison relies on a small number of daily observations (<3; Figure 3) that do not capture the monthly variation. Longer net-based time-series could improve the range of sampling conditions (e.g. duration, mesh size, depth) and reduce short snapshots which cannot reflect intra-annual variability.

We also note (as do the authors) that the global foraminifera biomass estimates of Schiebel and Movellan (2012) are somewhat

conservative as they focus on size fractions greater than 125  $\mu\text{m}$ . Considering size fractions >100  $\mu\text{m}$  allows for global planktic foraminifera biomass production to be two times higher, and including all size fractions (including juveniles), to be more than three times higher. Although this would bring our modelled estimate of 7.5 Tg C a little closer into alignment with data-based estimates, it does also raise the questions of what exactly we are comparing, with ForaminiferaEcoGenIE considering a single generic 190  $\mu\text{m}$  foraminifera group vs. the diversity of species and life stages in the real ocean. Increasing size diversity within the foraminifera functional type in the model would help, as would adding a life cycle, although the latter would be technically demanding.

### 3.1.3 | Connecting foraminifera's traits with their habitat

To explore how foraminifera distribution in the model depends on their traits and trade-offs, we compare the simulated foraminifera biogeography with their direct competitor, a generic zooplankton of the same size-class (190  $\mu\text{m}$ ; Table 1). The 190  $\mu\text{m}$  zooplankton differs from foraminifera in foraging (omnivore active feeder) as well as in growth rate as they do not have a calcification trade-off. In the model, this zooplankton group has a wider geographical range with higher biomass than foraminifera and in many regions, different seasonal patterns (Figures S1 and 2). This difference shows that foraminifera, as calcifiers and herbivorous passive feeders, are more limited by resource availability than non-calcifiers and active omnivorous feeders, which can alter their diet breadth depending on the spatial and temporal prey availability. Traits and associated trade-offs of calcification and herbivorous passive feeding are thus critical in controlling non-spinose foraminifera's distribution in the global ocean via resource competition.

Globally, our model shows a strong correlation between the abundance of foraminifera and the other plankton groups in the model (Table 2). That correlation suggests interspecies interactions to be the ecological driver of foraminifera distribution patterns. In the model, the interspecies interactions have a dynamic complex structure that changes at each time step. As such, each plankton group can affect foraminifera in different ways, depending on the bottom-up and top-down controls of the plankton community at the time. For example, the resource competition among phytoplankton can lead to strong or weak bottom-up effects on foraminifera, depending on which phytoplankton and zooplankton groups dominate the ecosystem at any time. Foraminifera's direct competitor for resources is the omnivorous microzooplankton group of the same size (190  $\mu\text{m}$ ). Depending on its concentration and prey preferences, the microzooplankton can outcompete foraminifera on resource competition and negatively affect foraminifera growth. In the model, the grazing pressure depends on the predator-prey size ratios and prey density. Thus, again, depending on the group densities at any



**TABLE 2** Table shows the Spearman's correlation coefficient (*r*) between foraminifera and environmental factors for the subpolar, mid-, and low latitudes and Indian Ocean biozones for pre-industrial and future pCO<sub>2</sub>

	Fe	PO <sub>4</sub>	SST	ph	Alk	sal	Picophyto	Nanophyto	Microphyto	Nanozoo	Microzoo	Mesozoo
<b>Subpolar (n = 98)</b>												
Pre-industrial	-0.2	-0.2	0.5	0.3	<0.1	0.4	0.7	-0.7	1.0	-0.1	0.7	0.9
RCP8.5 2050	-0.2	-0.3	0.6	0.1	<0.1	0.4	0.6	-0.6	0.9	-0.1	0.7	0.9
RCP8.5 2100	-0.1	<0.1	0.4	0.3	0.5	0.5	0.4	-0.3	0.9	0.1	0.6	0.8
<b>Mid-latitudes (n = 145)</b>												
Pre-industrial	0.6	0.9	-0.7	-0.3	0.4	<0.1	-0.8	0.9	0.9	0.5	0.7	0.8
RCP8.5 2050	0.5	0.9	-0.7	-0.1	0.3	-0.1	-0.8	0.9	0.9	0.6	0.8	0.9
RCP8.5 2100	0.4	0.9	-0.6	-0.2	0.2	-0.2	-0.8	0.9	1.0	0.7	0.8	0.9
<b>Low latitudes (n = 38)</b>												
Pre-industrial	0.2	<0.1	0.2	-0.1	0.2	0.3	-0.1	0.6	0.3	0.9	0.6	1.0
RCP8.5 2050	0.2	0.1	0.1	0.6	0.2	0.2	-0.1	0.5	0.4	0.8	0.6	0.9
RCP8.5 2100	0.2	0.2	0.1	0.6	0.1	0.1	-0.1	0.5	0.6	0.6	0.6	0.8
<b>Indian Ocean (n = 93)</b>												
Pre-industrial	0.3	0.8	-0.8	0.4	0.7	<0.1	-0.7	0.9	0.9	0.4	0.9	0.5
RCP8.5 2050	0.3	0.8	-0.8	-0.5	0.6	<0.1	-0.6	0.9	0.9	0.6	0.9	0.7
RCP8.5 2100	0.3	0.8	-0.8	-0.7	0.5	-0.1	-0.5	0.9	0.9	0.7	0.9	0.8

Note: In bold the *r* with *p* < .05. *n*, sample size (i.e. number of grids for which foraminifera's biomass concentration is higher than 10<sup>-9</sup> mmol C m<sup>-3</sup> for pre-industrial climate conditions (278 ppm CO<sub>2</sub>)).

time, the 190  $\mu\text{m}$  microzooplankton group can act as a protection against predation and have a positive effect on foraminifera growth. Since bottom-up and top-down controls have synergistic effects on foraminifera population, it is hard to determine whether a positive or negative correlation between the abundances of foraminifera and plankton groups reflects only bottom-up or top-down effects, respectively.

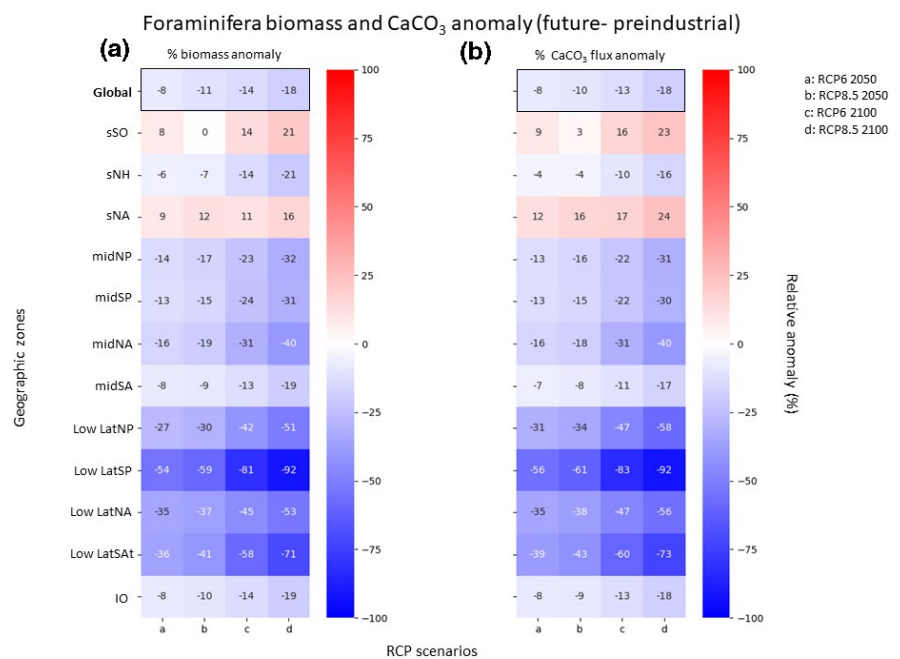
Depending on the region, we find that the abiotic parameters temperature and phosphate (the limiting nutrient for foraminifera's prey) exhibit the highest correlation coefficient with foraminifera abundance ( $r$ ; Table 2). Phosphate is the main abiotic driver of foraminifera's concentration for the Indian Ocean and mid-latitudes, followed by temperature. Temperature is the major abiotic driver of foraminifera distribution in the subpolar regions. Alkalinity and pH have a weak correlation with foraminiferal biomass, except for the Indian Ocean. However, we do not consider the role of these two factors any further as we do not explicitly model the calcification process that should have the strongest effect.

### 3.2 | Future projections of foraminifera biogeography, biomass, and calcification

The climate response to imposed increasing atmospheric  $\text{CO}_2$  concentrations in ForaminiferaEcoGENIE is characterized by a global and annual mean sea surface average (SST) warming of  $1.2^\circ\text{C}$  (RCP6) or  $1.4^\circ\text{C}$  (RCP8.5) by 2050, and  $2.1^\circ\text{C}$  (RCP6) or  $2.8^\circ\text{C}$  (RCP8.5) at 2100 (Figure S3). This climate response lies within the approximated  $\pm 1^\circ\text{C}$  spread of higher spatial resolution and fully coupled climate models, that project a model ensemble mean SST rise relative to year 1901 of  $3.2^\circ\text{C}$  (RCP8.5) by 2100; table 1 in Gattuso et al., 2015).

Globally, and for both scenarios, the projected changes in foraminifera abundance are strongly related to the overall dynamics of the simulated plankton community, showing that resource availability and competition remain the main drivers of distribution changes. In some regions, changes in temperature and phosphate also correlate strongly with foraminifera's biomass (Table 2). Foraminifera biomass drops 8%–11% by 2050 (RCP6 and RCP8.5, respectively) and 14%–18% by 2100. However, the changes are highly heterogeneous (Figures 2b and 5a). For instance, while the model predicts biomass losses for much of the global ocean, biomass increases are projected in the subpolar Southern Ocean by 8% (RCP6, 2050) to 21% (RCP8.5, 2100) and North Atlantic by 9% (RCP6, 2050) to 16% (RCP8.5, 2100; 2100, Figures 2b and 5a). In mid-latitudes and Indian Ocean, the biomass loss ranges from 8% (RCP6) to 10% (RCP8.5) in 2050 and 13% (RCP6) to 21% (RCP8.5) in 2100. Biomass reduction is higher in low latitudes reaching 35% in 2050 (RCP6) to 53% in 2100 (RCP8.5) in the Atlantic. In the low latitudes of South Pacific, the model projects extirpation of non-spinose foraminifera with concentration losses between 81% (RCP6) 92% (RCP 8.5, Figure 5a) by 2100.

Based on the projected changes in foraminifera organic carbon export and applying our preferred ( $10 \mu\text{g}$ ) conversion factor between organic and carbonate carbon described earlier, we project a global decrease in foraminifera  $\text{CaCO}_3$  flux of 8% (RCP6) to 10% (RCP8.5) by 2050 and 13% (RCP6)–18% (RCP8.5) by 2100 (Figure 5b). Again, there is a regional heterogeneity and the projected  $\text{CaCO}_3$  flux increases in subpolar North Atlantic and Southern Ocean. It is important to remember that these estimates do not consider any potential changes in foraminifera's biomineralization due to warming and acidification and are therefore likely conservative values (Fox et al., 2020; Lombard et al., 2010).



**FIGURE 5** Foraminifera relative (a) biomass concentration and (b) calcium carbonate export flux (futurepreindustrial) for RCP6 and RCP8.5. IO, Indian Ocean; LowLat NA, Low Latitude N. Atlantic; LowLat NP, Low Latitude N. Pacific; LowLat SA, Low Latitude S. Atlantic; LowLat SP, Low Latitude S. Pacific; midNA, mid-latitude N. Atlantic; midNP, mid-latitude N. Pacific; midSA, mid-latitude S. Atlantic; midSP, mid-latitude S. Pacific; pSO, polar Southern Ocean; sNA, subpolar North Atlantic; sNH, subpolar Northern Hemisphere; sSO, subpolar Southern Ocean

## 4 | DISCUSSION

Our study is the first trait-based approach to assess the global distribution and climate change sensitivity of non-spinose foraminifera. The ForamEcoGenIE model captures – to a first order – the modern biogeography of non-spinose foraminifera, with abundance increasing from low latitudes to coastal upwelling, temperate and subpolar environments. While our model overestimates the biomass compared to plankton net compilations in the first 80 m, our modelled foraminifera organic carbon production flux shows a better agreement with sediment traps. Model-data biases may arise from a lack of plasticity in the model calcification trade-offs, spatial and temporal sparsity in data, especially for highly undersampled parts of the Pacific, South Atlantic, and Indian Ocean, and very likely, because of the absence of fine-scale ocean dynamics and inter-annual variability. Due to sparse physiological and distribution data in temporal and spatial scales, it is unknown to us to what degree the model overestimates and the empirical observations underestimate the biomass stock and calcium carbonate flux at this point (Skogen et al., 2021). Additional empirical observations would aid the development of a large-scale zooplankton database which includes less abundant groups, such as foraminifera, enhance the model-data comparison, identify and help to overcome model limitations (Jonkers et al., 2021).

The absence of non-spinose forms in most oligotrophic regions in the model suggests that herbivory might not be an efficient-enough diet due to the limited food availability and strong resource competition with other zooplankton groups. This is supported by observations which show that in the oligotrophic (sub)tropics, non-spinose species complement their diet with detritus or small zooplankton (Bé & Tolderlund, 1971; Schiebel & Hemleben, 2017) and are symbiont facultative (Takagi et al., 2019). Laboratory studies have shown that symbiosis with autotrophic algae positively impacts planktonic foraminifera growth (e.g. Bé, 1982; Spero & De Niro, 1987). However, symbiotic relationships might increase the vulnerability of foraminifera to future warming as bleaching due to symbiont loss has been documented in the geological record (Edgar et al., 2013) akin to coral bleaching.

Our model does not capture foraminifera's standing stocks in the modern polar Southern Ocean. We speculate that this is due to the lack of an omnivorous/detritus diet of polar non-spinose species (Greco et al., 2021) or other polar traits such as dormancy (Dieckmann et al., 1991; Spindler & Dieckmann, 1986) and thermal tolerance. It is thus crucial that future studies include different foraging strategies and the symbiotic relationship with algae to study the foraminifera distribution and their potential vulnerability in the future.

Temperature has previously been considered the main driver of foraminifera distribution, followed by food availability, stratification, and carbonate saturation (Bé & Tolderlund, 1971; Ottens & Nederbragt, 1992; Schiebel et al., 2001, 2002; Schmidt, Renaud, et al., 2004; Storz et al., 2009). Sediment data have recorded community shifts in foraminifera related to temperature increases

occurring since pre-industrial times (Jonkers et al., 2019). It is important to note, though, that temperature is the environmental factor with the best data availability and proxy understanding (CLIMAP, 1976; Kucera et al., 2005; MARGO Project, 2009). Temperature has direct (e.g. enzymic activity, life span) and indirect (e.g. density and trait-mediated indirect interactions among species and populations) effects on their plasticity and distribution patterns. In contrast, many other environmental conditions which are indirectly correlated with temperature, such as prey density and carbonate saturation, are understudied. Our model highlights the importance of prey availability on foraminifera biogeography and the dynamics of the plankton community. We hypothesize that changes in temperature have indirect impacts on community structure as these modulate stratification, nutrient availability for phytoplankton, and therefore food for organisms higher up the food chain. As such, these changes are crucial for low biomass passive ambush herbivorous feeders, like foraminifera, which rely on nearby prey availability.

Under future warming scenarios, our study projects a biomass increase of non-spinose foraminifera in subpolar regions of the North Atlantic and the Southern Ocean and decrease elsewhere. This poleward shift has also been documented for many plankton groups over the last decades (Beaugrand et al., 2012; Hastings et al., 2020; Poloczanska et al., 2013). Only one other study has modelled planktonic foraminifera's distribution under future climate scenarios (RCP8.5), using the FORAMCLIM model (Roy et al., 2015). FORAMCLIM is calibrated on species' specific growth rates and non-spinose taxa are represented as herbivorous feeders. The foraminifera community depends on temperature and prey availability without resource competition or top-down control from other zooplankton. Despite the differences in modelling approaches between FORAMCLIM and ForamEcoGenIE (see Data S1 for more details), both models project similar changes in the distribution of non-spinose foraminifera (i.e. higher loss in the tropics and increase in (sub)polar regions). This increases our confidence in our understanding and shows that our selected traits and trade-offs allow future projections without being calibrated on taxon-specific physiological rates.

Changes in foraminifera distribution can impact the ocean inorganic carbon cycle via changes in ocean carbonate production. At low latitudes, non-spinose contribute approximately 1/3 to the foraminifera assemblage (Schmuker & Schiebel, 2002) and the calcium carbonate production is mainly driven by changes in the biomass of spinose species. The loss of non-spinose biomass and extirpation will remove this contribution to foraminifera calcium carbonate flux, despite those regions staying supersaturated with regards to calcite under both CO<sub>2</sub> emissions scenarios. At the same time, calcium carbonate export is projected to increase in the high-latitude regions, specifically the subpolar North Atlantic and the Southern Ocean. It is important to note that these regions are highly susceptible to changes in carbonate chemistry due to ice melt and they are naturally lower in carbonate saturation due to higher CO<sub>2</sub> gas solubility

in colder waters. This dissolution would exert a small but negative feedback on CO<sub>2</sub>. Should foraminifera reduce calcification rates in response to lower ambient carbonate saturation (Bijma et al., 1999; Lombard et al., 2010; Russell et al., 2004; Spero et al., 1997), this would further increase a negative stabilizing feedback on CO<sub>2</sub> and saturation. Still, foraminifera calcification process cannot be separated from their ecophysiology. Laboratory studies have shown that the prey type and amount influence calcification rates (Anderson et al., 1979; Spindler et al., 1984). Starvation leads to slower chamber formation and death, while overfeeding causes higher growth rates of cytoplasm, shell formation, and gametogenesis resulting in shorter life cycles (e.g. Anderson et al., 1979; Bé et al., 1981; Caron & Bé, 1984; Spindler et al., 1984). Therefore, a lack of prey could also influence carbonate production even under fully oversaturated conditions.

## 5 | CONCLUSIONS

We developed the first Earth System model which includes a trait-based ecosystem model of planktonic foraminifera. With this model, we assessed the environmental controls on modern non-spinose foraminifera and found that their distribution can be explained by the dynamics of the plankton community, followed by temperature and phosphate. In response to future climate change, the model suggests that the biomass of non-spinose foraminifera decreases by 8%–11% by 2050 and 14%–18% by 2100 (RCP6.5 and RCP8.5). Losses are not global though; shifts in the primary productivity to higher latitudes result in foraminifera biomass increasing in the sub-polar North Atlantic and Southern Ocean. The model projects that the non-spinose abundance will strongly reduce in low latitudes with an extirpation in the South Pacific by 2100. As a consequence of this biomass shift, we estimate that the calcium carbonate flux of non-spinose foraminifera will drop by 13%–18% by 2100 globally but with an increased flux at higher latitudes. A much deeper understanding of the physiological process of foraminifera calcification and relationship to environmental conditions via new field, laboratory and modelling studies, is clearly going to be necessary for refining projections of calcium carbonate production by foraminifera and hence future feedbacks on atmospheric CO<sub>2</sub>.

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## CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

## AUTHORS' CONTRIBUTIONS

Maria Grigoratou, Fanny M. Monteiro, Daniela N. Schmidt, and Andy Ridgwell designed the study. Maria Grigoratou, Fanny M. Monteiro, and Jamie D. Wilson developed the code. Maria Grigoratou run the simulations, performed the model, field data meta-analysis, and statistical analysis. Maria Grigoratou wrote the manuscript with the contribution of all authors.

## DATA AVAILABILITY STATEMENT

The ForamEcoGENIE code can be found here <https://github.com/derpycode/cgenie.muffin>.

The data and code for the statistical analysis and figures are publicly available and can be found online at <https://zenodo.org/record/5564573> (Grigoratou, Monteiro, Wilson, et al., 2021).

## REFERENCES

- Anderson, O. R., & Be, A. W. H. (1976). The ultrastructure of a planktonic foraminifer, *Globigerinoides sacculifer* (Brady), and its symbiotic dinoflagellates. *The Journal of Foraminiferal Research*, 6(1), 1–21. <https://doi.org/10.2113/gsjfr.6.1.1>
- Anderson, O. R., Spindler, M., Bé, A. W. H., & Hemleben, C. (1979). Trophic activity of planktonic foraminifera. *Journal of the Marine Biological Association of the United Kingdom*, 59, 791–799. <https://doi.org/10.1017/S002531540004577X>
- Barker, S., & Elderfield, H. (2002). Foraminiferal calcification response to glacial-interglacial changes in atmospheric CO<sub>2</sub>. *Science*, 297, 833–836. <https://doi.org/10.1126/science.1072815>
- Bé, A. W. H. (1982). Gametogenic calcification in a spinose planktonic foraminifer, *Globigerinoides sacculifer* (Brady). *Marine Micropaleontology*, 5, 283–310. [https://doi.org/10.1016/03778398\(80\)900146](https://doi.org/10.1016/03778398(80)900146)
- Bé, A. W. H., Caron, D. A., & Anderson, O. R. (1981). Effects of feeding frequency on life responses of the planktonic foraminifera *Globigerinoides sacculifer* in laboratory culture. *Journal of the Marine Biological Association of the United Kingdom*, 61(1), 257–277. <https://doi.org/10.1017/S002531540004604X>
- Bé, A. W. H., & Tolderlund, D. S. (1971). Distribution and ecology of planktonic foraminifera. In B. M. Funnell & W. R. Riedel (Eds.), *The micropaleontology of oceans* (pp. 105–150). Cambridge University Press. <https://doi.org/10.2307/1485406>
- Beaugrand, G., Mcquatters-gollop, A., Edwards, M., & Goberville, E. (2012). Long-term responses of North Atlantic calcifying plankton to climate change. *Nature Climate Change*, 3(3), 263–267. <https://doi.org/10.1038/nclimate1753>
- Beers, J. R., & Stewart, G. L. (1971). Micro-zooplankters in the plankton communities of the upper waters of the eastern tropical Pacific. *Deep Sea Research*, 18, 861–883. [https://doi.org/10.1016/0011-7471\(71\)90061-1](https://doi.org/10.1016/0011-7471(71)90061-1)
- Berger, W. H. (1969). Ecologic patterns of living planktonic Foraminifera. *Deep-Sea Research*, 16, 1–24. [https://doi.org/10.1016/0011-7471\(69\)90047-3](https://doi.org/10.1016/0011-7471(69)90047-3)
- Bijma, J., Spero, H. J., & Lea, D. W. (1999). Reassessing foraminiferal stable isotope geochemistry: Impact of the oceanic carbonate system (experimental results). In G. Fischer & G. Wefer (Eds.), *Uses of proxies in paleoceanography: Examples from the south Atlantic* (pp. 489–512). Springer Verlag.

- Brun, P., Stamieszkin, K., Visser, A. W., Licandro, P., Payne, M. R., & Kiørboe, T. (2019). Climate change has altered zooplankton-fuelled carbon export in the North Atlantic. *Nature Ecology & Evolution*, 3, 416–423. <https://doi.org/10.1038/s41559-018-0780-3>
- Buitenhuis, E. T., Le Quééré, C., Bednaršek, N., & Schiebel, R. (2019). Large contribution of pteropods to shallow CaCO<sub>3</sub> export. *Global Biogeochemical Cycles*, 33(3), 458–468. <https://doi.org/10.1029/2018GB006110>
- Buitenhuis, E. M., Vogt, R., Moriarty, N., Bednarsek, S. C., Doney, S. C., Leblanc, K., Le Quééré, C., Luo, Y. W., O'Brien, C., O'Brien, T., Peloquin, J., Schiebel, R., & Swan, C. (2013). MAREDAT: Towards a world atlas of MARine Ecosystem DATA. *Earth System Science Data, Copernicus Publications*, 5, 227–239. <https://doi.org/10.5194/essd-5-227-2013>
- Caron, D. A., & Bé, A. W. H. (1984). Predicted and observed feeding rates of the spinose planktonic foraminifer *Globigerinoides sacculifer*. *Bulletins of Marine Science*, 35, 1–10.
- CLIMAP Project Members. (1976). The surface of the ice-age Earth. *Science*, 191, 1131–1137. <https://doi.org/10.1126/science.191.4232.1131>
- Davis, C. V., Badger, M. P. S., Bown, P. R., & Schmidt, D. N. (2013). The response of calcifying plankton to climate change in the Pliocene. *Biogeosciences*, 10(9), 6131–6139. <https://doi.org/10.5194/bg-10-6131-2013>
- De Moel, H., Ganssen, G. M., Peeters, F. J. C., Jung, S. J. A., Kroon, D., Brummer, G. J. A., & Zeebe, R. E. (2009). Planktic foraminiferal shell thinning in the Arabian sea due to anthropogenic ocean acidification? *Biogeosciences*, 6(9), 1917–1925. <https://doi.org/10.5194/bg-6-1917-2009>
- Dieckmann, G. S., Spindler, M., Lange, M. A., Ackley, S. F., & Eicken, H. (1991). Antarctic sea ice: A habitat for the foraminifer *Neogloboquadrina pachyderma*. *Journal of Foraminiferal Research*, 21(2), 182–189. <https://doi.org/10.2113/gsjfr.21.2.182>
- Dutkiewicz, S., Cermenó, P., Jahn, O., Follows, M. J., Hickman, A. E., Taniguchi, D. A. A., & Ward, B. A. (2020). Dimensions of marine phytoplankton diversity. *Biogeosciences*, 17, 609–634. <https://doi.org/10.5194/bg-17-609-2020>
- Dutkiewicz, S., Scott, J. R., & Follows, M. J. (2013). Winners and losers: Ecological and biogeochemical changes in a warming ocean. *Global Biogeochemical Cycles*, 27(2), 463–477. <https://doi.org/10.1002/gbc.20042>
- Edgar, K. M., Bohaty, S. M., Gibbs, S. J., Sexton, P. F., Norris, R. D., & Wilson, P. A. (2013). Symbiotic 'bleaching' in planktic foraminifera during the Middle Eocene Climatic Optimum. *Geology*, 41(1), 15–18. <https://doi.org/10.1130/G33388.1>
- Ehrlich, E., & Gaedke, U. (2018). Not attackable or not crackable—how pre- and post-attack defences with different competition costs affect prey coexistence and population dynamics. *Ecology and Evolution*, 13(8), 6625–6637. <https://doi.org/10.1002/ece3.4145>
- Field, D. B. (2004). Variability in vertical distributions of planktonic foraminifera in the California Current: Relationships to vertical ocean structure. *Paleoceanography*, 19, PA2014. <https://doi.org/10.1029/2003PA000970>
- Field, D. B., Baumgartner, T. R., Charles, C. D., Ferreira-Bartrina, V., & Ohman, M. (2006). Planktonic foraminifera of the California Current reflect 20th century warming. *Science*, 311, 63–66. <https://doi.org/10.1126/science.1116220>
- Flynn, K. J., St John, M., Raven, J. A., Skibinski, D. O. F., Allen, J. I., Mitra, A., & Hofmann, E. E. (2015). Acclimation, adaptation, traits and trade-offs in plankton functional type models: Reconciling terminology for biology and modelling. *Journal of Plankton Research*, 37, 683–691. <https://doi.org/10.1093/plankt/fbv036>
- Follows, M. J., Dutkiewicz, S., Grant, S., & Chisholm, S. W. (2007). Emergent biogeography of microbial in a model ocean. *Science*, 315(5820), 1843–1846. <https://doi.org/10.1126/science.1138544>
- Fox, L., Stukins, S., Hill, T., & Miller, C. G. (2020). Quantifying the effect of anthropogenic climate change on calcifying plankton. *Scientific Reports*, 10, 1620. <https://doi.org/10.1038/s41598-020-58501-w>
- Frankignoulle, M., Canon, C., & Gattuso, J. P. (1994). Marine calcification as a source of carbon dioxide: Positive feedback of increasing atmospheric CO<sub>2</sub>. *Limnology and Oceanography*, 39(2), 458–462. <https://doi.org/10.4319/lo.1994.39.2.0458>
- Gattuso, J.-P., Magnan, A., Bille, R., Cheung, W. W. L., Howes, E. L., Joos, F., Allemand, D., Bopp, L., Cooley, S. R., Eakin, C. M., Hoegh-Guldberg, O., Kelly, R. P., Poertner, H.-O., Rogers, A. D., Baxter, J. M., Laffoley, D., Osborn, D., Rankovic, A., Rochette, J., ... Turley, C. (2015). Contrasting futures for ocean and society from different anthropogenic CO<sub>2</sub> emissions scenarios. *Science*, 349(6243). <https://doi.org/10.1126/science.aac4722>
- Greco, M., Morard, R., & Kucera, M. (2021). Single-cell metabarcoding reveals biotic interactions of the Arctic calcifier *Neogloboquadrina pachyderma* with the eukaryotic pelagic community. *Journal of Plankton Research*, 43(2), 113–125. <https://doi.org/10.1093/plankt/fbab015>
- Grigoratou, M., Monteiro, F. M., Ridgwell, A., & Schmidt, D. N. (2021). Investigating the benefits and costs of spines and diet on planktonic foraminifera distribution with a trait-based ecosystem model. *Marine Micropaleontology*, 166. <https://doi.org/10.1016/j.marmicro.2021.102004>
- Grigoratou, M., Monteiro, F. M., Schmidt, D. N., Wilson, J. D., Ward, B. A., & Ridgwell, A. (2019). A trait-based modelling approach to planktonic foraminifera ecology. *Biogeosciences*, 16(7), 1469–1492. <https://doi.org/10.5194/bg-16-1469-2019>
- Grigoratou, M., Monteiro, F. M., Wilson, J. D., Ridgwell, A., & Schmidt, D. N. (2021). ForamEcoGenE: Foramecogenie\_paper\_v1.0.0. *Zenodo*. <https://zenodo.org/record/5564573>
- Harvell, C. D. (1990). The evolution of inducible defence. *Parasitology*, 100(S1), S53–S61. <https://doi.org/10.1017/S0031182000073017>
- Hastings, R. A., Rutterford, L. A., Freer, J. J., Collins, R. A., Simpson, S. D., & Genner, M. J. (2020). Climate change drives poleward increases and equatorward declines in marine species. *Current Biology*, 30(8), 1572–1577. <https://doi.org/10.1016/j.cub.2020.02.043>
- Hecht, A. D. (1976). An ecologic model for test size variation in recent planktonic foraminifera; applications to the fossil record. *Journal of Foraminiferal Research*, 6(4), 295–311. <https://doi.org/10.2113/gsjfr.6.4.295>
- Henderson, G. M. (2002). New oceanic proxies for paleoclimate. *Earth and Planetary Science Letters*, 203, 1–13. [https://doi.org/10.1016/S0012-821X\(02\)00809-9](https://doi.org/10.1016/S0012-821X(02)00809-9)
- Jonkers, L., Hillebrand, H., & Kucera, M. (2019). Global change drives modern plankton communities away from the pre-industrial state. *Nature*, 570, 372–375. <https://doi.org/10.1038/s41586-019-1230-3>
- Jonkers, L., Meilland, J., Rillo, M. C., de Garidel-Thoron, T., Kitchener, J. A., & Kucera, M. (2021). Linking zooplankton time series to the fossil record ICES. *Journal of Marine Science*, 1–8. <https://doi.org/10.1093/icesjms/fsab123>
- Kiørboe, T. (2011). How zooplankton feed: Mechanisms, traits and trade-offs. *Biological Reviews*, 86(2), 311–339. <https://doi.org/10.1111/j.1469-185X.2010.00148.x>
- Kiørboe, T., Visser, A., & Andersen, K. H. (2018b). A trait-based approach to ocean ecology. *ICES Journal of Marine Science*, 75(6), 1849–1863. <https://doi.org/10.1093/icesjms/fsy090>

- Kucera, M., Weinelt, M., Kiefer, T., Pflaumann, U., Hayes, A., Weinelt, M., Chen, M.-T., Mix, A. C., Barrows, T. T., Cortijo, E., Duprat, J., Juggins, S., & Waelbroeck, C. (2005). Reconstruction of sea-surface temperatures from assemblages of planktonic foraminifera: Multi-technique approach based on geographically constrained calibration data sets and its application to glacial Atlantic and Pacific Oceans. *Quaternary Science Reviews*, 24, 951–998. <https://doi.org/10.1016/j.quascirev.2004.07.014>
- Lombard, F., da Rocha, R. E., Bijma, J., & Gattuso, J.-P. (2010). Effect of carbonate ion concentration and irradiance on calcification in planktonic foraminifera. *Biogeosciences*, 7, 247–255. <https://doi.org/10.5194/bg-7-247-2010>
- MARGO Project Members, Waelbroeck, C., Paul, A., Kucera, M., Rosell-Melé, A., Weinelt, M., Schneider, R., Mix, A. C., Abelmann, A., Armand, L., Bard, E., Barker, S., Barrows, T. T., Benway, H., Cacho, I., Chen, M. T., Cortijo, E., Crosta, X., de Vernal, A., ... Turon, J. L. (2009). Constraints on the magnitude and patterns of ocean cooling at the Last Glacial Maximum. *Nature Geosciences*, 2, 127–132. <https://doi.org/10.1038/ngeo411>
- Marsh, R., Müller, S. A., Yool, A., & Edwards, N. R. (2011). Incorporation of the C-GOLDSTEIN efficient climate model into the GENIE framework: “eb\_go\_gs” configurations of GENIE. *Geoscientific Model Development*, 4, 957–992. <https://doi.org/10.5194/gmd-4-957-2011>
- Meinshausen, M., Smith, S. J., Calvin, K., Daniel, J. S., Kainuma, M. L. T., Lamarque, J.-F., Matsumoto, K., Montzka, S. A., Raper, S. C. B., Riahi, K., Thomson, A., Velders, G. J. M., & van Vuuren, D. P. (2011). The RCP greenhouse gas concentrations and their extensions from 1765 to 2300. *Climatic Change*, 109, 213–241. <https://doi.org/10.1007/s10584-011-0156-z>
- Moy, A. D., Howard, W. R., Bray, S. G., & Trull, T. W. (2009). Reduced calcification in modern Southern Ocean planktonic foraminifera. *Nature Geoscience*, 2(4), 276–280. <https://doi.org/10.1038/ngeo460>
- Ottens, J. J., & Nederbragt, A. J. (1992). Planktic foraminiferal diversity as indicator of ocean environments. *Marine Micropaleontology*, 19, 13–28. [https://doi.org/10.1016/0377-8398\(92\)90019-G](https://doi.org/10.1016/0377-8398(92)90019-G)
- Poloczanska, E. S., Brown, C. J., Sydeman, W. J., Kiessling, W., Schoeman, D. S., Moore, P. J., Brander, K., Bruno, J. F., Buckley, L. B., Burrows, M. T., Duarte, C. M., Halpern, B. S., Holding, J., Kappel, C. V., O'Connor, M. I., Pandolfi, J. M., Parmesan, C., Schwing, F., Thompson, S. A., & Richardson, A. J. (2013). Global imprint of climate change on marine life. *Nature Climate Change*, 3, 919–925. <https://doi.org/10.1038/nclimate1958>
- Rebotim, A., Voelker, A. H. L., Jonkers, L., Waniek, J. J., Meggers, H., Schiebel, R., Fraile, I., Schulz, M., & Kucera, M. (2017). Factors controlling the depth habitat of planktonic foraminifera in the subtropical eastern North Atlantic. *Biogeosciences*, 14(4), 827–859. <https://doi.org/10.5194/bg-14-827-2017>
- Ridgwell, A., Schmidt, D. N., Turley, C., Brownlee, C., Maldonado, M. T., Tortell, P., & Young, J. R. (2009). From laboratory manipulations to Earth system models: Scaling calcification impacts of ocean acidification. *Biogeosciences*, 6, 2611–2623. <https://doi.org/10.5194/bg-6-2611-2009>
- Ridgwell, A., & Zeebe, R. E. (2005). The role of the global carbonate cycle in the regulation and evolution of the Earth system. *Earth and Planetary Science Letters*, 234(3–4), 299–315. <https://doi.org/10.1016/j.epsl.2005.03.006>
- Roy, T., Lombard, F., Bopp, L., & Gehlen, M. (2015). Projected impacts of climate change and ocean acidification on the global biogeography of planktonic Foraminifera. *Biogeosciences*, 12, 2873–2889. <https://doi.org/10.5194/bg-12-2873-2015>
- Russell, A. D., Hönisch, B., Spero, H. J., & Lea, D. W. (2004). Effects of seawater carbonate ion concentration and temperature on shell U, Mg, and Sr in cultured planktonic foraminifera. *Geochimica et Cosmochimica Acta*, 68(21), 4347–4361. <https://doi.org/10.1016/j.gca.2004.03.013>
- Schiebel, R. (2002). Planktic foraminiferal sedimentation and the marine calcite budget. *Global Biogeochemical Cycles*, 16(4), 3–1–3–21. <https://doi.org/10.1029/2001GB001459>
- Schiebel, R., & Hemleben, C. (2005). Modern planktic foraminifera. *Paläontologische Zeitschrift*, 79(1), 135–148. <https://doi.org/10.1007/BF03021758>
- Schiebel, R., & Hemleben, C. (2017). Planktic foraminifera in the modern ocean, Chapter 4: Nutrition, Symbionts, and Predators, p. 154, Chapter 7: Ecology, 209–220, Chapter 10: Methods, 313–315, Springer-Verlag, Berlin Heidelberg. <https://doi.org/10.1007/978-3-662-50297-6>
- Schiebel, R., & Movellan, A. (2012). First-order estimate of the planktic foraminifer biomass in the modern ocean. *Earth System Science Data*, 4, 75–89. <https://doi.org/10.5194/essd-4-75-2012>
- Schiebel, R., Waniek, J., Bork, M., & Hemleben, C. (2001). Planktic foraminiferal production stimulated by chlorophyll redistribution and entrainment of nutrients. *Deep-Sea Research Part I*, 48, 721–740. [https://doi.org/10.1016/S0967-0637\(00\)00065-0](https://doi.org/10.1016/S0967-0637(00)00065-0)
- Schiebel, R., Waniek, J., Zeltner, A., & Alves, M. (2002). Impact of the Azores Front on the distribution of planktic foraminifera, shelled gastropods, and coccolithophorids. *Deep-Sea Research Part II*, 49, 4035–4050. [https://doi.org/10.1016/S0967-0645\(02\)00141-8](https://doi.org/10.1016/S0967-0645(02)00141-8)
- Schmidt, D. N., Renaud, S., Bollmann, J., Schiebel, R., & Thierstein, H. R. (2004). Size distribution of Holocene planktic foraminifer assemblages: Biogeography, ecology and adaptation. *Marine Micropaleontology*, 50, 319–338. [https://doi.org/10.1016/S0377-8398\(03\)00098-7](https://doi.org/10.1016/S0377-8398(03)00098-7)
- Schmidt, D. N., Thierstein, H. R., Bollmann, J., & Schiebel, R. (2004). Abiotic forcing of plankton evolution in the Cenozoic. *Science*, 303, 207–210. <https://doi.org/10.1126/science.1090592>
- Schmuker, B., & Schiebel, R. (2002). Planktic foraminifera and hydrography of the eastern and northern Caribbean Sea. *Marine Micropaleontology*, 46(3–4), 387–403. [https://doi.org/10.1016/S0377-8398\(02\)00082-8](https://doi.org/10.1016/S0377-8398(02)00082-8)
- Siccha, M., & Kucera, M. (2017). ForCenS, a curated database of planktonic foraminifera census counts in marine surface sediment samples. *Scientific Data*, 4, 17109. <https://doi.org/10.1038/sdata.2017.109>
- Skogen, M. D., Ji, R., Akimova, A., Daewel, U., Hansen, C., Hjøllø, S. S., van Leeuwen, S. M., Maar, M., Macias, D., Mousing, E. A., Almroth-Rosell, E., Saille, S. F., Spence, M. A., Troost, T. A., & van de Wolfshaar, K. (2021). Disclosing the truth: Are models better than observations? *Marine Ecology Progress Series*, DYNMODav1. <https://doi.org/10.3354/meps13574>
- Spero, H. J., Bijma, J., Lea, D. W., & Bernis, B. E. (1997). Effect of seawater carbonate concentration on foraminiferal carbon and oxygen isotopes. *Nature*, 390(6659), 497–500. <https://doi.org/10.1038/37333>
- Spero, H. J., & De Niro, M. J. (1987). The influence of symbiont photosynthesis on the  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  values of planktonic foraminiferal shell calcite. *Symbiosis*, 4(213), 228.
- Spindler, M., & Dieckmann, G. S. (1986). Distribution and abundance of the planktic foraminifer *Neogloboquadrina pachyderma* in sea ice of the Weddell Sea (Antarctica). *Polar Biology*, 5, 185–191. <https://doi.org/10.1007/BF00441699>
- Spindler, M., Hemleben, C., Salomons, J. B., & Smit, L. P. (1984). Feeding behaviour of some planktonic foraminifera in laboratory cultures. *Journal of Foraminiferal Research*, 14, 237–249. <https://doi.org/10.2113/gsjfr.14.4.237>
- Storz, D., Schulz, H., Waniek, J. J., Schulz-Bull, D. E., & Kučera, M. (2009). Seasonal and interannual variability of the planktic foraminiferal flux in the vicinity of the Azores Current. *Deep Sea Research Part*

- I, *Oceanographic Research Papers*, 56(1), 107–124. <https://doi.org/10.1016/J.DSR.2008.08.009>
- Takagi, H., Kimoto, K., Fujiki, T., Saito, H., Schmidt, C., Kucera, M., & Moriya, K. (2019). Characterizing photosymbiosis in modern planktonic foraminifera. *Biogeosciences*, 16, 3377–3396. <https://doi.org/10.5194/bg-16-3377-2019>
- Vallat, R. (2018). Pingouin: Statistics in Python. *Journal of OpenSource Software*, 3(31), 1026. <https://doi.org/10.21105/joss.01026>
- Ward, B. A., Dutkiewicz, S., Jahn, O., & Follows, M. J. (2012). A size-structured food-web model for the global ocean. *Limnology and Oceanography*, 57(6), 1877–1891. <https://doi.org/10.4319/lo.2012.57.6.1877>
- Ward, B. A., Wilson, J. D., Death, R. M., Monteiro, F. M., Yool, A., & Ridgwell, A. (2018). EcoGENIE 1.0: Plankton ecology in the cGENIE Earth system model. *Geoscientific Model Development*, 11(10), 4241–4267. <https://doi.org/10.5194/gmd-11-4241-2018>
- Weinkauf, M. F. G., Kunze, J. G., Waniek, J. J., & Kučera, M. (2016). Seasonal variation in shell calcification of planktonic foraminifera in the NE atlantic reveals species-specific response to temperature, productivity, and optimum growth conditions. *PLoS One*, 1–33. <https://doi.org/10.1371/journal.pone.0148363>
- Zarkogiannis, S. D., Antonarakou, A., Tripathi, A., Kontakiotis, G., Mortyn, P. G., Drinia, H., & Greaves, M. (2019). Influence of surface ocean density on planktonic foraminifera calcification. *Science Reports*, 9, 533. <https://doi.org/10.1038/s41598-018-36935-7>

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