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Spatially Heterogeneous Responses of Planktonic Foraminiferal Assemblages Over 700,000 Years of Climate Change

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ABSTRACT

Aim: To determine the degree to which assemblages of planktonic foraminifera track thermal conditions.

Location: The world's oceans.

Time Period: The last 700,000 years of glacial–interglacial cycles.

Major Taxa Studied: Planktonic foraminifera.

Methods: We investigate assemblage dynamics in planktonic foraminifera in response to temperature changes using a global dataset of Quaternary planktonic foraminifera, together with a coupled Atmosphere–Ocean General Circulation Model (AOGCM) at 8000-year resolution. We use 'thermal deviance' to assess assemblage responses to climate change, defined as the difference between the temperature at a given location and the bio-indicated temperature (i.e., the abundance-weighted average of estimated temperature optima for the species present).

Results: Assemblages generally tracked annual mean temperature changes through compositional turnover, but thermal deviances are evident under certain conditions. The coldest-adapted species persisted in polar regions during warming but were not joined by additional immigrants, resulting in minimal assemblage turnover. The warmest-adapted species persisted in equatorial regions during cooling with similarly minimal assemblage change. Assemblages at mid-latitudes mostly tracked temperature cooling and warming.

Main Conclusions: Planktonic foraminiferal assemblages were generally able to track or endure temperature changes: as climate warmed or cooled, bio-indicated temperature also became warmer or cooler, although to a variable degree. At polar sites under warming and at equatorial sites under cooling, the change in bio-indicated temperature was less than, or even opposite to, what would be expected from estimated environmental change. Nevertheless, all studied species persisted across the study interval, regardless of thermal deviance—a result that highlights the resilience and inertia of planktonic foraminifera on an assemblage level to the last 700,000 years of climate change.

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1 | Introduction

Anthropogenic climate change is threatening marine ecosystems (Cooley et al. 2022). Marine species commonly respond to climate change by shifting their distribution to follow suitable conditions (Chen et al. 2011; Lenoir et al. 2020; Pinsky et al. 2013; Poloczanska et al. 2013; Yasuhara and Deutsch 2022). However, the degree to which marine species are able to keep pace with current rates of climate change via dispersal remains uncertain (García Molinos et al. 2016; Munday et al. 2013). Although individual species of marine ectotherms are projected to closely track their thermal limits (Sunday, Bates, and Dulvy 2012), assemblages are unlikely to respond cohesively to climate change (García Molinos et al. 2016; Walther et al. 2002), which can be attributed to the differential needs and tolerances of individual species across multiple abiotic parameters (Strack et al. 2022). The individualistic responses of species to climate change may make certain regions more prone to assemblage changes than others (Reddin et al. 2022; Stuart-Smith et al. 2015). Such differential responses can be indicated by a discrepancy between ambient temperatures and the average of conditions preferred by individual species within assemblages (i.e., thermal deviance; Devictor et al. 2012; Menéndez et al. 2006; Svenning and Sandel 2013). However, the paucity of long-term studies prevent a full understanding of projected assemblage changes in response to climate change (Rosenzweig et al. 2008). Mismatches between existing conditions and average temperature preferences of the assemblage constituents have been studied more in terrestrial than marine ecosystems (Sunday, Bates, and Dulvy 2011). Terrestrial ecosystems often have more dispersal barriers than marine systems as well as containing species with lower vagility (Burgess et al. 2016). Thus, conclusions from global change biology studies in the terrestrial realm may not always translate to the marine realm (Knapp et al. 2017).

The exceptional fossil record of planktonic foraminifera renders them an ideal system to investigate thermal deviances in the ocean. Planktonic foraminifera are a near-ubiquitous component of the marine zooplankton. Their calcite shells (tests) are well-preserved in seafloor sediments, allowing for the composition of marine assemblages to be quantified at high temporal and spatial resolution. The tests of planktonic foraminifera have been used to investigate climatic and ecological changes in both modern and fossil systems (Antell et al. 2021; Ezard et al. 2011; Jonkers, Hillebrand, and Kucera 2019; Morard et al. 2015; Yasuhara et al. 2012; Yasuhara, Wei, et al. 2020).

Modern planktonic foraminiferal assemblages have changed in community structure as a response to anthropogenic climate warming (Jonkers, Hillebrand, and Kucera 2019; Yasuhara, Huang, et al. 2020). The fossil record provides complementary data on how species have responded to various magnitudes, rates and directions of climate change. Since unique combinations of climatic variables existed in the past (Williams and Jackson 2007) and are projected to emerge in the future (Burke et al. 2018; Lotterhos, Láruson, and Jiang 2021; Williams, Jackson, and Kutzbach 2007), critical information can be obtained from the fossil record on biotic responses to climate conditions outside modern human experience. The continuous nature of the planktonic foraminifera microfossil record, with its high temporal and spatial resolution, provides an opportunity to study the impacts of climate change on spatiotemporal assemblage patterns at a temporal scale relevant for modern-day global change biology (e.g., Hutchins and Fu 2017; Jonkers et al. 2022).

Here we investigated the degree to which planktonic foraminiferal assemblages changed over the past 700,000 years of glacial–interglacial cycles. We based our analysis on a global dataset of Quaternary planktonic foraminifera records at 8-thousand-year (ka) resolution, coupled with surface temperature data from a global circulation model. For each foraminiferal assemblage, we calculated thermal deviance as the difference between the modelled temperature at the location and the 'bio-indicated temperature' for the local assemblage, quantified as the abundance-weighted average across estimated temperature optima of the individual species' distributions (Figure 1). We then used generalised additive and generalised linear models to quantify thermal deviance as a function of temperature change both globally and within latitudinal bands (low, mid and high latitudes). We further linked these patterns to changes in compositional turnover, latitudinal diversity and the probability of local extinction (extirpation) in response to climate change.

2 | Material and Methods

2.1 | Fossil Data

Foraminiferal occurrence data over the last 700 ka are from Antell et al. (2021), which were derived from Fenton et al. (2021). These records consist of curated and taxonomically harmonised planktonic foraminifera occurrences with recent age models sourced from the PANGAEA Open Access library (Diepenbroek et al. 2002), ocean drilling projects (DSDP, ODP and IODP), the Neptune database (Renaudie, Lazarus, and Diver 2020) and the ForCens database (Siccha and Kucera 2017). We removed occurrences from depositional sites with shallow depths [< 100 m depth, following Antell et al. 2021], since fossils from these sites have a higher probability of being transported from their life position. We retained those sites with information about the relative abundance of individual species and with occurrences in at least 10 consecutive time intervals globally. The final dataset contained 55 species with 38,441 occurrences from 1955 sites (see Appendix S1 Table S1).

Occurrence records were binned into 88 time bins of 8-ka resolution, from the recent subfossil record to 704 ka, following Antell et al. (2021). The chosen bin duration allowed for imprecision in fossil ages, typically on the order of a few thousand years (Martin 1999), and agrees with the resolution of the coupled Atmosphere–Ocean General Circulation Model outputs (4 ka) and with time-averaging expected in fossil assemblages of planktonic foraminiferal assemblages (see Martin 1999). The bin duration also ensures ecological dynamics were captured at a higher resolution than the fluctuations from glacial minima to interglacial maxima.

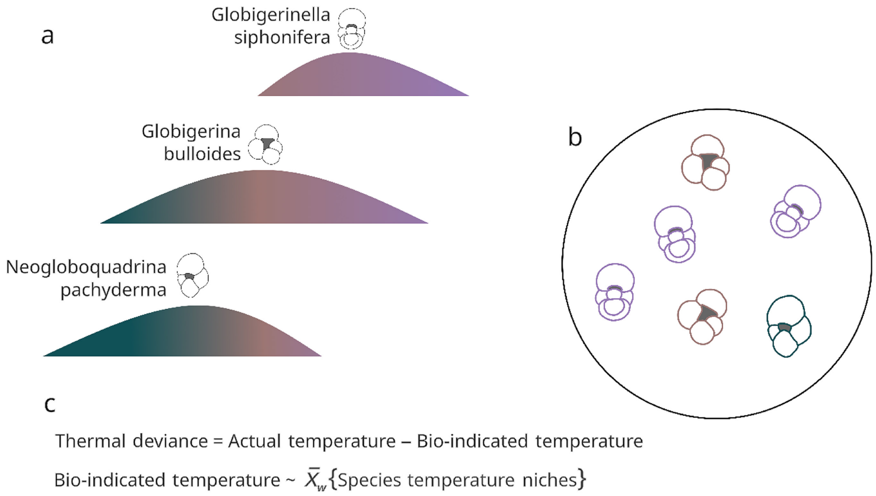

FIGURE 1 | Calculation of the thermal deviance of a planktonic foraminiferal assemblage. (a) Individual planktonic foraminifera species occupy a specific temperature niche. This temperature niche can be estimated for each species by documenting the response of fossil foraminifera species along the univariate axis of mean annual temperature. (b) An assemblage of planktonic foraminifera consists of various species, each displaying a characteristic temperature niche. The temperature of an assemblage ('bio-indicated temperature') can be estimated by weighted averaging the temperature niches of individual species via an ecological transfer function ($\bar{x}_w$), which takes both species' composition and relative abundance of species into account. (c) The thermal deviance of the assemblage is then quantified as the difference between the modelled temperature at the location of the assemblage and the bio-indicated temperature of the assemblage.

We use the term 'assemblage' to refer to all species present within a sediment sample (i.e., a single location on Earth) in a given time bin. The final dataset contains 2607 assemblages (see Appendix S1 Table S2).

2.2 | Temperature Data

Temperature is likely the single most important explanatory variable structuring the geographic distributions of planktonic foraminifera (Morey, Mix, and Pisias 2005; Rillo, Woolley, and Hillebrand 2022). One way to reconstruct both spatial and temporal temperature information for prehistoric oceans is using coupled Atmosphere–Ocean General Circulation Models (AOGCMs). We used mean annual sea surface temperature (MAT) from Antell et al. (2021), extracted from the UK Met Office Hadley Centre Coupled Model (Valdes et al. 2017). This model family is known to perform well in capturing mean climate state in the past (Flato et al. 2014; Reichler and Kim 2008; Valdes et al. 2017). The precise model configuration is documented in Valdes et al. (2017). Climate data were downscaled to 1.25° × 1.25° horizontal resolution at 20 vertical ocean levels following Antell et al. (2021), from which we used the surface layer to extract MAT, a surface–subsurface layer from 78 m water depth and subsurface layer from 164 m water depth. These temperature layers were then used to extract temperature data at depth preferences of individual species (see below).

Fossil occurrence data were paired with AOGCM climate data from the midpoint of time bins (e.g., climate was modelled at 12 ka for occurrences binned from 16 to 8 ka). Per-assemblage temperature change was calculated as the difference in estimated MAT at an assemblage location from the previous time bin to the time bin of the assemblage. This means that temperature change was always calculated over the same time period, as defined by the model's temporal resolution, rather than varying according to gaps in the foraminifera data. Temperature change was, therefore, defined locally at the site of the sediment core, providing a best estimate of climate changes experienced by the assemblage. We additionally repeated analyses (i) at a global scale with temperature data derived from palaeo-proxies, (ii) in the high latitudes with temperature data derived from palaeo-proxies and (iii) with AOGCM temperature data derived at depth preferences of individual species (see below).

2.3 | Statistical Analysis

2.3.1 | Thermal Deviance

We calculated the preferred temperature of each foraminiferal species using an ecological transfer function in the 'rioja' R package version 0.9–26 (Juggins 2020). We used weighted averaging partial least squares (WA-PLS) regression and calibration (Ter Braak et al. 1993) to infer past environmental preferences of planktonic foraminiferal assemblages across MAT at the sea surface. Performance of the WA-PLS transfer function was determined using a leave-one-out cross-validation (see Appendix S1 Figure S1). WA-PLS requires the development of a calibration dataset, which is then used to model the relationship between assemblages and temperature. We calibrated the WA-PLS function using all planktonic foraminiferal occurrences of the final dataset.

We additionally calibrated the WA-PLS function on subsets of the data, focused only on (i) samples from the core top, (ii) samples falling within the interquartile range of all temperature variation throughout the last 700 ka and (iii) samples falling outside the interquartile range (see Appendix S1 Figure S2). We calibrated the WA-PLS function on these subsets to test whether calculation of the optimum temperature of each foraminiferal species is strongly dependent on the choice of underlying calibration data. In addition to sea surface MAT estimates used in the main analysis, we extracted temperature estimates from each species' preferred depth. We derived information on each species' modern depth range from Antell et al. (2021, Table S2 therein) and assigned a depth preference as one of the following: surface (40 m in the AOGCM), surface–subsurface (78 m) or subsurface (164 m). WA-PLS was then used to re-estimate the preferred temperature of each foraminiferal species.

We define thermal deviance as the difference between the temperature at a given location (as estimated by the AOGCM) and the 'bio-indicated temperature', which is the average of the species' temperature optima within an assemblage, weighted by relative abundances (Figure 1). Deviance is positive when the actual water temperature is warmer than the bio-indicated temperature. Previous studies have used the term 'climatic debt' for this metric to quantify lags between biotic responses of plants, birds and butterflies to contemporary climate changes (Bertrand et al. 2016; Devictor et al. 2012; Gaüzère, Princé, and Devictor 2017). The same metric has been noted as 'thermal bias' (Stuart-Smith et al. 2015), 'community-climate lag' (Blonder et al. 2017) or 'community-climate mismatch' (Bonachela, Burrows, and Pinsky 2021). However, the notation of 'debt', 'lag', 'bias' or 'mismatch' might imply that populations occupy suboptimal climate conditions, which is likely not applicable to planktonic organisms. We, therefore, use the term 'thermal deviance' throughout this study.

Thermal deviance calculated by WA-PLS takes the relative abundance of individual species into account. We also estimated thermal deviance based on presence–absence changes in species within assemblages (see Appendix S1 Figures S3 and S4). To do so, we calculated a species' temperature preference as the average temperature of the species' range based on all occurrences of that species across time bins. For a given assemblage, the assemblage temperature was calculated as the average of all species' temperature preferences. Thermal deviance was then calculated as the difference in assemblage bio-indicated temperature and the surface temperature estimate based on the AOGCM. The resulting estimates for the thermal deviance were, therefore, only based on presence–absence changes of individual species and do not take the relative abundance of species within assemblages into account.

We modelled the average thermal deviance across sites in a time bin as a function of temperature change using a generalised additive model fitted via the 'mgcv' R package version 1.8.41 (Wood, Pya, and Säfken 2016) and identified change points using the first derivative of the model function. Within latitudinal zones, the trend in thermal deviance was estimated using a linear model. We distinguished three latitudinal zones based on absolute latitude. Between 0° and 30° is defined as low latitude; between 30° and 60° as mid-latitude; and above 60° as high latitude. We acknowledge that using absolute latitudes, which merges the Northern and Southern Hemispheres, may introduce biases in the results, particularly for taxa predominantly restricted to one hemisphere, since species with hemispheric preferences may exhibit distinct patterns in turnover dynamics. We, therefore, repeated our analysis by categorising latitudinal zones (i.e., mid, high and low) within hemispheres (see Appendix S1 Figure S5).

Using the depth-specific estimates for each species, we additionally modelled thermal deviance separately for each depth layer and latitudinal zone using linear models (see Appendix S1 Figure S6). Assemblages for these models were defined as those species present within a sediment core in a given time bin and given depth habitat. Bio-indicated temperatures of these depth-assemblages were compared to the local temperature change of the same depth layer, with temperature change calculated as the difference in estimated AOGCM temperature from the temporal bin of the assemblage to the previous temporal bin, similar to the sea surface temperature analysis. The thermal deviance of each assemblage was then modelled as a function of temperature change, with an individual linear model for each combination of depth habitat and latitudinal zone. Each model, therefore, estimated the thermal deviance at a given depth habitat (surface, surface–subsurface or subsurface) within a latitudinal zone (mid, high or low).

As a sensitivity analysis, we repeated our modelling steps for thermal deviance using linear mixed effect models in the lme4 R package version 1.1-30 (Bates et al. 2015). In this approach, we specified temporal bin as a random effect (see Appendix S1 Figure S7), treating bins as samples of a larger population to account for variability and differences across bins. Additionally, we fitted a first-order autoregressive model to estimate latitudinal trends in thermal deviance, accounting for temporal non-independence (see Appendix Table S3). We further tested whether the substantially increased number of samples towards the recent affected our results by repeating our analysis on a subset of data that omitted samples from the most recent time bin, containing the highest number of samples (1901 of 2607 assemblages; see Appendix S1 Figures S7–S9).

2.3.2 | Compositional Turnover

We were interested in the relationship between degree of compositional turnover and climate change through time and space. We, therefore, calculated compositional turnover at each latitudinal zone across consecutive time bins. We grouped all assemblages occurring in the same temporal bins and latitudinal zone together and calculated turnover against all assemblages of the same latitudinal zone of the previous bin. Turnover was assessed by dissimilarity indices with the 'vegan' R package version 2.6.2 (Oksanen et al. 2020) based on the Chi-squared coefficient (Prentice 1980) and the Bray–Curtis dissimilarity index (see Appendix Table S4). We then modelled turnover per site and temporal bin as a function of per-latitudinal zone temperature change using linear models.

2.3.3 | Species Richness and Extirpation Probability

To test for changes in species richness with climate change, we counted the number of species per latitudinal zone for each temporal bin and modelled this proxy of species richness as a function of temperature change using linear models.

To test whether high thermal deviances correspond to local extinctions for individual species within assemblages, we quantified the average extirpation probability for each latitudinal zone under instances of climate warming and climate cooling. For this analysis, we counted the number of species that were present in a latitudinal zone in temporal bin *i* but not in the subsequent temporal bin $i+1$. We additionally noted whether the temperature change was above zero (i.e., climate warming) or below zero (i.e., climate cooling) from temporal bin *i* to temporal bin $i+1$ for the focal latitudinal zone. The extirpation probability was then modelled in a time-continuous logistic regression for all temporal bins and summarised per climate scenario (i.e., warming and cooling).

2.3.4 | Temperature Sensitivity Analysis

We calculated thermal deviance for planktonic foraminiferal assemblages based on the mean annual surface temperature estimate of the AOGCM for the main-text results. As both the assemblage bio-indicated temperature and the temperature reconstructions are based on AOGCMs, we additionally tested whether the same patterns were observed on a global level when using a recent compilation of palaeo-proxy data for temperature reconstructions (Friedrich and Timmermann 2020). The palaeo-proxy data spanned the last 125 ka and were converted to the same resolution as our assemblage data by averaging proxy values for the temporal bins of the assemblage data (i.e., upscaling or aggregation). We tested whether taking a point estimate for the temperature reconstruction biased our results by iteratively sampling the age estimates of the palaeo-proxy data from the entire distribution, including the temperature estimates for the mean age ±4 ka (see Appendix S1 Figure S10), which corresponds to the temporal uncertainty of our fossil data.

We repeated our analysis for the high-latitudinal zone using temperature estimates for North Atlantic surface temperatures from Mg/Ca ratios in *Globigerina bulloides* for the past 12 ka (Farmer, Chapman, and Andrews 2008). This palaeo-proxy data was at centennial resolution, which we converted to the same resolution of our foraminiferal assemblage data by taking the mean of all palaeo-proxy estimates falling in the same temporal bin as the assemblage. We then fitted linear fixed effects model for warming and cooling, respectively, and compared the results to those based on the AOGCM reconstructions (see Appendix S1 Figure S7).

3 | Results

3.1 | Global Thermal Deviance

Planktonic foraminiferal assemblages generally tracked temperature changes over the past 700,000 years. However, assemblages showed little compositional change when temperature changes were below ca. 0.3°C, which resulted in thermal deviances between the actual temperature at the site and the bio-indicated temperature of the assemblage (Figure 2b). Under larger temperature changes (>0.3°C), thermal deviances remained nearly unchanged (Figure 2b).

Our results remain consistent when using global temperature estimated from palaeo-proxies instead of modelled AOGCM temperature estimates (Appendix S1 Figure S10), indicating that the relationships described here are not an artefact of using AOGCM output for both the modelled temperature and the thermal deviance estimates.

3.2 | Thermal Deviance Across Latitudes

The response of planktonic foraminiferal assemblages to temperature change through time was spatially heterogeneous (Figure 2c, Appendix S1 Table S3). Assemblages at high latitudes showed only moderate thermal deviance during climate cooling but accumulated substantial thermal deviance with warming (Figure 2c). With every 1°C warming, average bio-indicated temperatures of high-latitude assemblages were 3.7°C lower than the actual temperature at the site (95% CI [1.8°C, 5.5°C]; Appendix S1 Table S3). Conversely, assemblages at low latitudes exhibited higher thermal deviances under climatic cooling and smaller deviances when temperatures increased. With every 1°C cooling, average temperature preferences of low-latitude assemblages were 3.3°C warmer than the site temperature (95% CI [1.6°C, 3.8°C]; Appendix S1 Table S3). Assemblages at mid-latitudes closely tracked temperature cooling and showed a modest increase in thermal deviance (<1°C) under warming.

Using various data subsets for the estimation of the ecological transfer function (see Appendix S1 Figure S2) and omitting data from time bins that showed indications of higher or lower sampling intensity (see Appendix S1 Figure S4) produced the same overall patterns of spatially heterogeneous responses to temperature change (Figure 3). Similarly, using a mixed effect model with a random effect of temporal bin resulted in the same patterns (Appendix S1 Figure S7). Main results were also corroborated by autoregressive models accounting for temporal dependence (Appendix S1 Table S3). Patterns remained consistent when defining latitudinal zones within hemispheres (Appendix S1 Figure S5).

Using temperature estimates derived at each species' preferred depth layer to model thermal deviance resulted in the same trends as for surface temperature, apart from mid-latitude assemblages during climate cooling (see Appendix S1 Figure S6). High-latitude assemblages showed large increases in thermal deviance during climate warming, and low-latitude assemblages during cooling. Mid-latitude assemblages, however, showed larger increases in thermal deviance during cooling compared to those estimated using surface temperature.

Calculating thermal deviance on occurrences instead of relative abundance of individual foraminifera species revealed the same trends but generally higher magnitudes of thermal deviance at both the global scale (see Appendix S1 Figure S3) and within latitudinal bands (see Appendix S1 Figure S4).

Our results remain consistent when using local temperature estimates from palaeo-proxies for the high-latitudinal zone, rather than modelled AOGCM temperature estimates (Appendix S1 Figure S7), demonstrating that the relationships

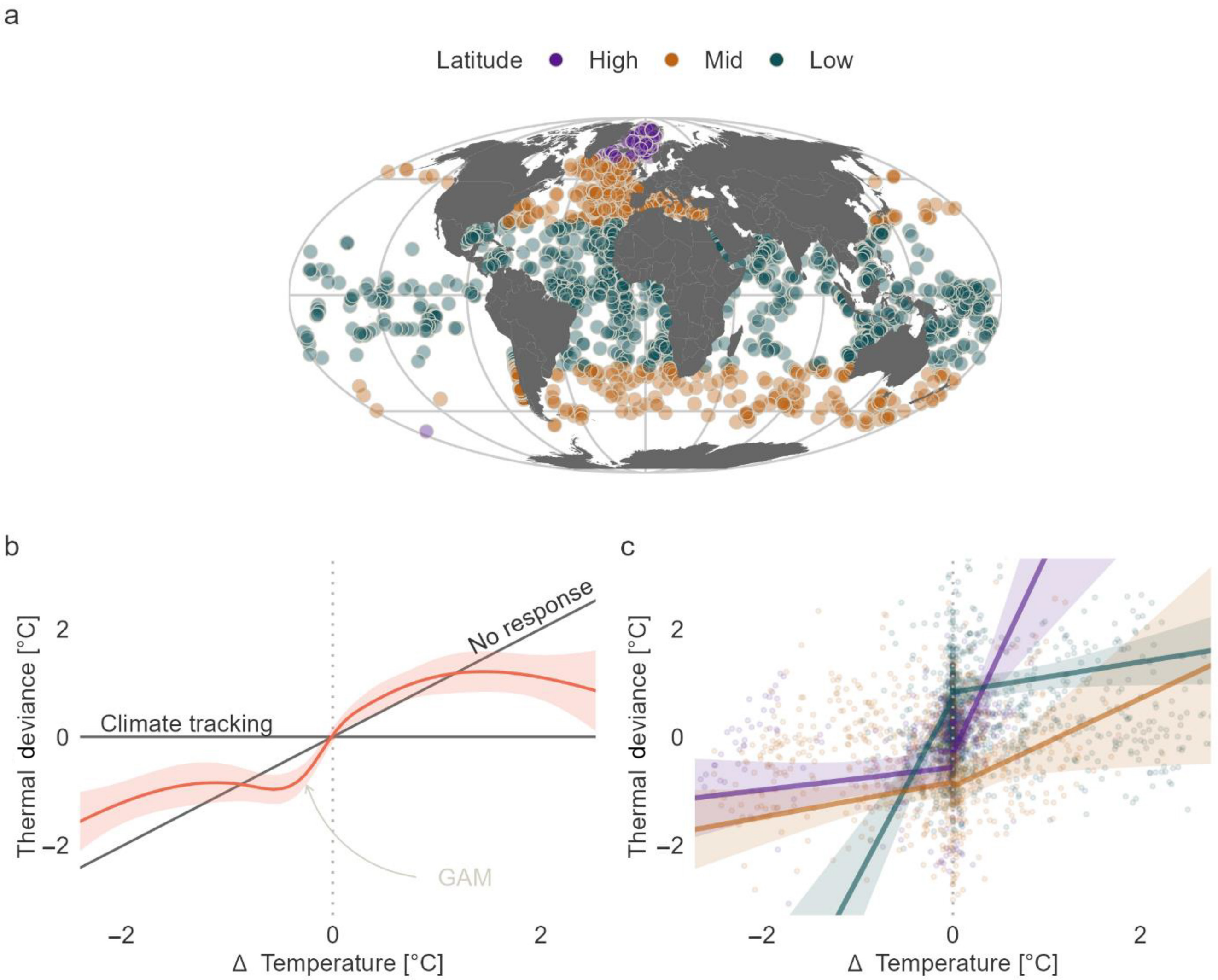

FIGURE 2 | (a) Global distribution of foraminiferal assemblages used in this work, coloured by latitudinal zones, 0°–30°, 30°–60°, 60°–90°. (b) On a global level, a generalised additive model (GAM) predicts thermal deviance for each assemblage as a function of estimated local temperature change from the previous temporal bin. The deviation is itself the difference between coeval local temperature estimated from Earth systems models (AOGCM) versus the temperature expected based on assemblage composition and abundance. The horizontal line shows a one-to-one relationship between AOGCM temperature and bio-indicated temperature (e.g., 1°C warming corresponds to a bio-indicated temperature that is 1°C warmer, resulting in no thermal deviance). The 'no response' line shows a constant bio-indicated temperature regardless of AOGCM temperature change. (c) Latitudinal patterns of thermal deviance as a function of temperature change. The coloured areas depict the 95% confidence interval of the focal trend based on linear regression models. A positive deviation corresponds to bio-indicated temperatures adjusting to be cooler than expected from Earth systems model temperature estimates, and a negative deviation to warmer bio-indicated temperatures than expected.

we describe are not merely a by-product of using AOGCM data for both the modelled temperature and the thermal deviance calculations.

3.3 | Compositional Turnover

Compositional turnover increased for mid-latitude assemblages with increasing magnitude of temperature change under both warming and cooling scenarios (Figure 4a, Appendix S1 Table S4). This was not the case for high- and low-latitude assemblages. High-latitude assemblages showed an increase in compositional turnover during climate cooling but not during climate warming, where compositional turnover generally decreased (Figure 2c, Appendix S1 Table S4). In contrast, low-latitude assemblages showed slightly increased compositional turnover with climate warming and minimal changes in compositional turnover with climate cooling. We obtained similar results using the more traditional Bray–Curtis dissimilarity index instead of Chi-squared coefficients (see Appendix S1 Table S4).

3.4 | Species Richness and Extirpation Probability

Species richness was highest in low-latitudinal zones and lowest in high-latitudinal zones (Figure 4b). Species richness generally did not increase or decrease during climate changes (see Appendix S1 Table S5).

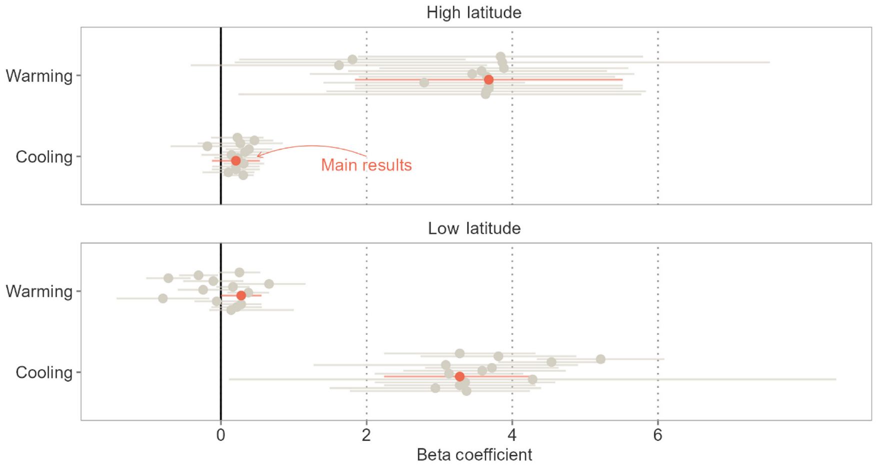

FIGURE 3 | Results for the global thermal deviance of all foraminiferal assemblages as a function of temperature change (beta coefficient and 95% confidence interval). The red estimates are reported in the main text and are based on the full data set and fixed effects regression models. The grey estimates are based on robustness tests using alternative training datasets for the ecological transfer function (see Appendix S1 Figure S2), alternative definitions of latitudinal zones (see Appendix S1 Figure S5), a depth habitat approach (see Appendix S1 Figure S6), subsets of data that show indication of higher or lower sampling intensity (see Appendix S1 Figure S7), and sea surface estimates from an independent proxy instead of AOGCM output (see Appendix S1 Figure S7).

We found no substantial differences in extirpation probabilities between cooling and warming scenarios for all latitudinal zones (Figure 4c). Average extirpation probability was highest in mid-latitude assemblages and lowest in high-latitude assemblages (see Appendix S1 Table S5).

4 | Discussion

Our findings suggest that assemblages of planktonic foraminifera track temperature changes, which is congruent with existing literature on marine microfossils on global (Strack et al. 2022; Yasuhara et al. 2012, 2017; Yasuhara, Wei, et al. 2020) and local spatial scales (Bond et al. 1997; Field et al. 2006; Hüls and Zahn 2000). However, assemblages tolerate modest temperature changes (< 0.3°C) with little change in species' composition. Additionally, under climate warming, more cold-adapted species were found in polar assemblages than predicted by a linear, one-to-one relationship between water temperature and bio-indicated temperature. We also observed a disproportionate abundance of warm-adapted species in low-latitude assemblages under a climate cooling scenario. These results are consistent with the persistence and survival of species with the highest or lowest temperature preferences, regardless of the magnitude of climate change over glacial–interglacial cycles. At mid-latitudes, the bio-indicated temperatures of assemblages mirrored the corresponding temperature change more closely.

These latitudinally heterogeneous responses of assemblages to temperature change can be linked to observed patterns in compositional turnover (Figure 4a). At a given site undergoing warming, more warm-adapted species are expected to move to the site (or increase their local abundance) and more cold-adapted species are expected to go locally extinct (or decrease their local relative abundance), and *vice versa* for cooling (e.g., Chen et al. 2011). Both processes contribute to turnover. In accordance with these expectations, we observed an increase in compositional turnover in mid and low-latitude assemblages with warming (Figure 4a). In contrast, compositional turnover tends to decrease or stay constant with magnitude of warming in high-latitude assemblages, increasing the observed thermal deviance of high-latitude assemblages under climate warming (Figure 2c). Similarly, while compositional turnover increases during climate cooling for high- and mid-latitude assemblages as expected, turnover is constant for low-latitude assemblages, resulting in an increasing thermal deviance for the latter.

Intriguingly, our findings diverge from patterns observed in modern marine fisheries (Burrows et al. 2019; Cheung, Watson, and Pauly 2013). Bio-indicated temperatures of fish catch were found to be significantly and positively related to regional changes in sea surface temperature, with an increasing dominance of catches of warm-adapted species at higher latitudes and a decrease in the proportion of catches of subtropical species in the tropics. This is in line with predictions of a domino effect where warm-adapted species migrate poleward with climate warming, potentially driving extinctions of polar endemics (Yasuhara and Deutsch 2022). In contrast, our results show that cold-adapted foraminifera species persist in higher latitudes under warming, with only a few warm-adapted species migrating into polar regions, resulting in high thermal deviance.

Our results hence highlight the resilience and inertia of planktonic foraminiferal assemblages to climate change. Modest temperature changes are likely to have remained within the thermal tolerance limits of many species within an assemblage (see Appendix S1 Table S3), such that species did not experience pressure to shift their distributions or abundance, resulting in compositional stability at the assemblage level. We observed this for temperature changes below 0.3°C per 8 ka on a global level (Figure 2b). It is important to note, however, that time-averaging and uncertainty in the estimated bio-indicated temperatures could influence these observations.

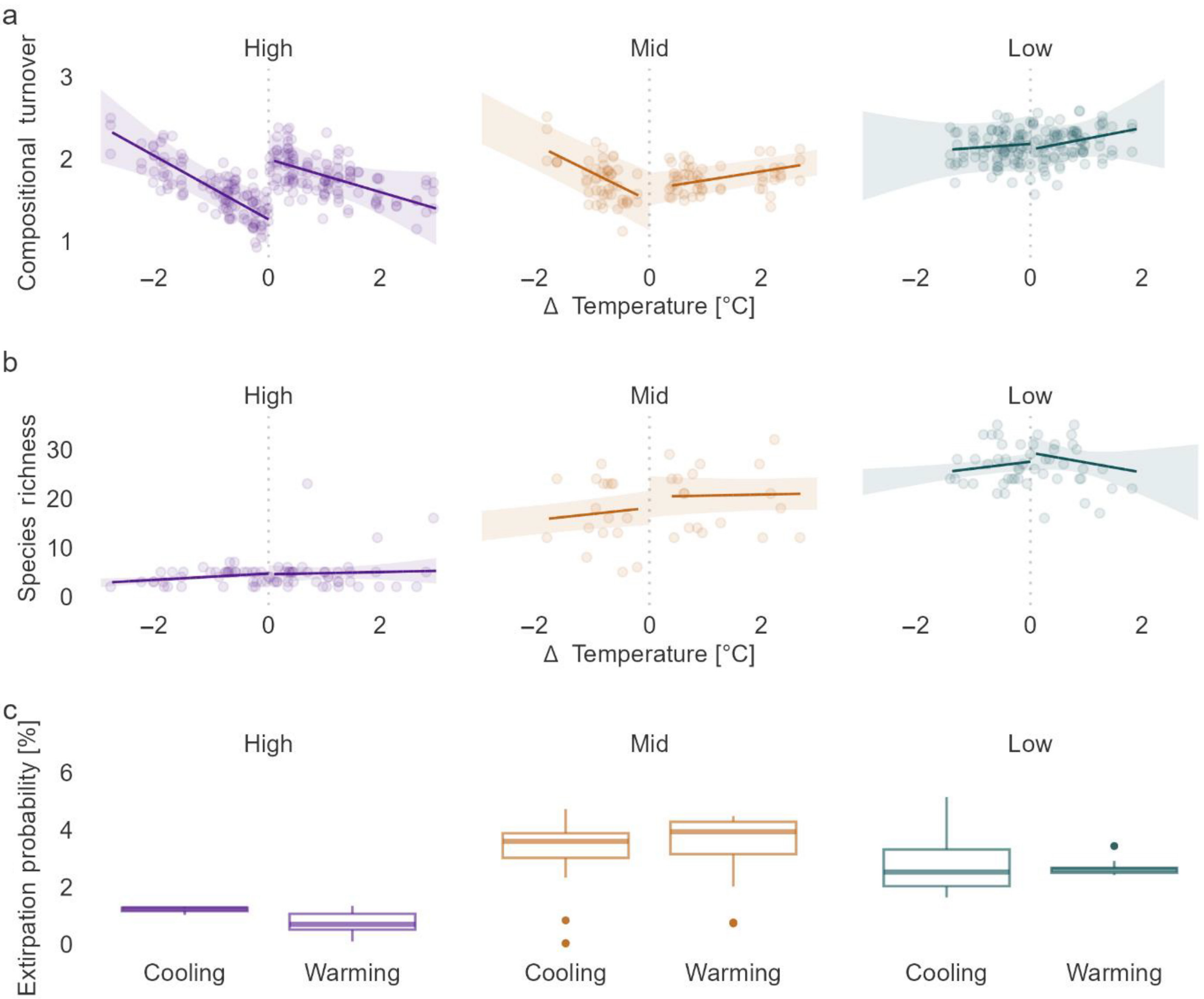

FIGURE 4 | Changes in assemblage composition as a response to temperature changes. (a) Compositional turnover for each latitudinal zone based on Chi-squared dissimilarity indices for each assemblage. (b) The number of species within each latitudinal zone. (c) Extirpation probability as modelled by the binomial signal of remaining species against species that experienced extirpation in an assemblage through time (see Methods). The bold lines in (a) and (b) depict the regression slopes across data points, and the shaded area the corresponding 95% confidence intervals.

Under larger temperature changes (> 0.3°C), the persistence of high-latitude assemblages during climate warming and low-latitude assemblages during climate cooling (Figure 2c) did not lead to increased extirpation risk (Figure 4c). This can be attributed to several potential, non-mutually exclusive mechanisms. First, thermal conditions might always remain within the thermal tolerance limits of the coldest- and warmest-adapted species. These species might be able to survive wide deviations from their thermal optimum, for instance by remodelling their physiology (Seebacher, White, and Franklin 2015). Alternatively, thermal heterogeneity at small spatial scales and/or across a depth gradient may provide microhabitats suitable for species at current locations, even as regional average temperatures begin to change (Fuller et al. 2010; Kretschmer et al. 2018). While planktonic foraminifera harbouring photosymbionts may be more constrained in their suitable vertical distribution by light availability, all planktonic species have some leeway to vary their depth distribution and thereby moderate exposure to large-scale changes in environmental condition (Rebotim et al. 2017).

Regardless of the underlying mechanism for the observed resilience and inertia, our results suggest that planktonic foraminiferal assemblages possess great capacity for stability in the face of climate perturbations of up to 3.2°C absolute temperature change and may show less reshuffling of ecosystem structure under anthropogenic warming than previously anticipated (e.g., Chen et al. 2011; Yasuhara and Deutsch 2022). However, high resilience may only partially explain the decreasing turnover of high-latitude assemblages during climate warming (Figure 4a). While interspecific competition is unlikely to impede species immigration (Rillo et al. 2019), factors such as sea ice cover, seasonality, ocean chemistry and light availability may contribute to the observed pattern (Zamelczyk et al. 2021). We, therefore, emphasise that the relationship between thermal deviance, extirpation risk and turnover may depend on numerous ecological and environmental factors, underscoring the complexity of foraminiferal assemblage responses to climate change.

An alternative explanation for the observed latitudinal signal in thermal deviance could be that modelled temperature estimates from the AOGCM are directionally biased, such that thermal deviances are emerging erroneously from the climate model output. Prior studies suggest such errors in palaeoclimate models may be localised, for example to the North Atlantic during glacial intervals (Jonkers et al. 2023). Thus, although imprecision in estimated sea temperature exists in our study, it is improbable that it explains the observed patterns of at high latitudes under warming and, conversely, at low latitudes under cooling, as well as the consistency of results under various robustness tests (see Figure 3 and Material and Methods and Results section).

Our results further highlight the importance of *within-community* relative abundance changes for explaining species' responses to temperature change. We found lower thermal deviances when relative abundance changes were included, indicating species responded to warming or cooling through substantial abundance changes within an assemblage. Novel plankton communities, such as those described since the last ice age (Strack et al. 2022), could, therefore, result from both habitat tracking and significant shifts in the relative abundance of species within their current ranges. Both mechanisms—shifts in geographical ranges and changes in relative abundance within communities—should be incorporated when assessing the biotic response to temperature change.

We emphasise that our results only estimate compositional changes of assemblages as a function of temperature. Although temperature is likely the single most important explanatory variable structuring the geographic distributions of planktonic foraminifera (Fenton et al. 2016; Yasuhara, Wei, et al. 2020), other environmental parameters can affect species' turnover, particularly in waters above 25°C (Rillo, Woolley, and Hillebrand 2022). The high thermal deviance of low-latitude assemblages under cooling reported here might, therefore, result from a decoupling of temperature and species' turnover dynamics in warm ecosystems due to the increased importance of other environmental factors such as net primary productivity or post-depositional dissolution effects, indicated by water depth (Rillo, Woolley, and Hillebrand 2022). Using the results reported here to estimate future compositional change of planktonic assemblages, for example, under anthropogenic climate change, requires careful consideration of potential interacting environmental parameters and temporal scales. Nevertheless, our results can be taken to suggest that planktonic foraminifera, and perhaps other planktonic organisms, are generally able to closely track temperature changes, albeit with spatially distinct responses of high- and low-latitude assemblages.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data and code files are publicly available at: https://doi.org/10.6084/m9.figshare.26379217.v1. All analyses were carried out in R v.4.1.2 (R Core Team 2023). We used the 'tidyverse' collection of R packages (Wickham et al. 2019) to transform and visualise data.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.