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RESEARCH ARTICLE

Coherent response of zoo- and phytoplankton assemblages to global warming since the Last Glacial Maximum

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Abstract

Aim: We are using the fossil record of different marine plankton groups to determine how their biodiversity has changed during past climate warming comparable to projected future warming.

Location: North Atlantic Ocean and adjacent seas. Time series cover a latitudinal range from 75° N to 6° S.

Time period: Past 24,000 years, from the Last Glacial Maximum (LGM) to the current warm period covering the last deglaciation.

Major taxa studied: Planktonic foraminifera, dinoflagellates and coccolithophores.

Methods: We analyse time series of fossil plankton communities using principal component analysis and generalized additive models to estimate the overall trend of temporal compositional change in each plankton group and to identify periods of significant change. We further analyse local biodiversity change by analysing species richness, species gains and losses, and the effective number of species in each sample, and compare alpha diversity to the LGM mean.

Results: All plankton groups show remarkably similar trends in the rates and spatio-temporal dynamics of local biodiversity change and a pronounced non-linearity with climate change in the current warm period. Assemblages of planktonic foraminifera and dinoflagellates started to change significantly with the onset of global warming around 15,500 to 17,000 years ago and continued to change at the same rate during the current warm period until at least 5000 years ago, while coccolithophore assemblages changed at a constant rate throughout the past 24,000 years, seemingly irrespective of the prevailing temperature change.

Main conclusions: Climate change during the transition from the LGM to the current warm period led to a long-lasting reshuffling of zoo- and phytoplankton assemblages, likely associated with the emergence of new ecological interactions and possibly a shift in the dominant drivers of plankton assemblage change from more abiotic-dominated causes during the last deglaciation to more biotic-dominated causes with the onset of the Holocene.

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KEYWORDS
biodiversity, coccolithophores, dinoflagellate cysts, last deglaciation, microfossils, planktonic foraminifera

1 | INTRODUCTION

Current global warming is already affecting global marine biodiversity (Antão et al., 2020) and is expected to have a stronger effect in the future (Beaugrand et al., 2015; García Molinos et al., 2016; Nolan et al., 2018). Understanding the response of marine organisms to climate change is an important yet challenging task as biodiversity dynamics are influenced by simultaneous processes of geographic range shifts, local extinction, as well as speciation on longer time scales (i.e. hundreds of thousands to millions of years). These processes may be further affected by ecological drift, natural selection via interacting biotic and abiotic variables in conjunction with dispersal ability (Vellend, 2010). On shorter time scales (i.e. thousands of years), in order for species to persist in a changing environment, they can either adapt to the new environment or disperse, shifting their distributions (habitat tracking; Brett et al., 2007). Indeed, the potential for high adaptation rates on short time scales has been shown for different marine plankton species (Bach et al., 2018; Geerts et al., 2015; Lohbeck et al., 2012; Padfield et al., 2016). Also, geographical range shifts have been observed in many species across different environments (for reviews see Parmesan, 2006; Poloczanska et al., 2013; Root et al., 2003; Walther et al., 2002) and are especially common in marine plankton due to their high dispersal potential in an environment with fewer physical barriers than in the terrestrial realm (Lenoir et al., 2020; Poloczanska et al., 2013). Considering the complexity of the marine realm and the multilayered interactions between local species and their environment, migrating species will experience new direct and indirect ecological interactions (Van der Putten et al., 2010). Furthermore, range shifts in response to environmental change may vary among species and occur at varying pace, resulting in the potential emergence of novel assemblages that are different from those that existed before the environmental change (Antão et al., 2020; Chen, Hill, et al., 2011; García Molinos et al., 2016; Poloczanska et al., 2013).

Given these different and complex ways in which taxa can reassemble in response to environmental change, it is difficult to predict how current communities will change with current and future climate change. Observational records can help us in these predictions; however, longitudinal ecology studies rarely span more than 100 years (Dornelas et al., 2018), resulting in small observed environmental change compared to the expected magnitude of future anthropogenic global warming. The fossil record can expand this observational window. In particular, sedimentary records of eukaryotic microplankton that produce microfossils have a high potential to serve as archives to study the species response to past climate change of comparable magnitude to projected future anthropogenic global warming (Rillo et al., 2021; Yasuhara, Huang, et al., 2020). Even though the marine plankton consists mainly of soft-bodied organisms with low fossilization potential (Buitenhuis et al., 2013), several plankton groups secrete resistant organic or inorganic remains that are preserved in the sediment and the resulting fossil assemblages can be reliable indicators of the biodiversity of the living assemblages (Kidwell, 2001; Tomašových & Kidwell, 2009; Yasuhara et al., 2012). Many marine plankton groups that are preserved in the sediment record have been shown to be sensitive to ongoing climate change (coccolithophores: Rost & Riebesell, 2004; diatoms and dinoflagellates: Hinder et al., 2012; planktonic foraminifera: Jonkers et al., 2019) and can therefore be used to study past biodiversity changes in response to climate change. The microfossil record has been widely used to reconstruct past climate change, resulting in a wealth of data from past time slices and time series (de Vernal et al., 2005; Gersonde et al., 2005; Kucera, Rosell-Melé, et al., 2005; Kucera, Weinelt, et al., 2005). However, their potential to reveal biodiversity changes across continuous periods of environmental change has been less explored.

Recently, Strack et al. (2022) used the fossil record of planktonic foraminifera to study their relationship to climate change during the past 24 thousand years (kyr) on a basin-wide scale (North Atlantic Ocean). During this period, the world transitioned from the Last Glacial Maximum (LGM) to the current warm period (i.e. the Holocene). Planktonic foraminifera assemblages started to change with the onset of global warming, but their shift continued during the current warm period, when climate change was less pronounced (Strack et al., 2022). One explanation for this prolonged assemblage change into the established warm period is a shift in the drivers of species assembly from more abiotic causes during the last deglaciation (i.e. temperature change) to more biotic causes during the beginning of the Holocene (i.e. species interactions). These results were based only on planktonic foraminifera, a group of zooplankton. It is important to investigate the generality of these results—whether these observed biodiversity dynamics during the last deglaciation also happened in other plankton groups. For instance, phytoplankton ecology is generally characterized by higher species richness, shorter generation times and potentially other environmental drivers than zooplankton ecology, and so phytoplankton groups may differ from planktonic foraminifera in their relationship to climate change.

To assess how other groups of plankton besides planktonic foraminifera changed in relation to climate change during the last deglaciation, we here also study the relationship of fossil dinoflagellates and coccolithophores. Not all dinoflagellates are fossilisable, but about 13%–16% of dinoflagellate species produce organic-walled resting cysts which are preserved in the sediment (Head, 1996). All three plankton groups show a strong modern latitudinal diversity gradient in the North Atlantic Ocean with lowest diversities at the highest latitudes and a peak in diversity in the mid-latitudes rather than the equatorial region (planktonic foraminifera: Fenton et al., 2016, 2023; Rutherford et al., 1999; Tittensor et al., 2010; Yasuhara, Wei, et al., 2020; dinoflagellate cysts: Chen, Irwin, & Finkel, 2011; coccolithophores: Boeckel & Baumann, 2008; O'Brien et al., 2016). By considering dinoflagellates and coccolithophores alongside planktonic foraminifera, our study design includes plankton groups that differ in their diversity, trophic strategy and preservation (Table 1). Also, the groups differ in terms of their ecological importance and functions and they play vital roles in the global food webs with dinoflagellates and coccolithophores being primary producers. Understanding how these plankton groups responded to past climate change is important in assessing the fate of trophic resources that are fundamental to the future of humanity and may provide valuable policy-relevant information on future anthropogenic climate change impacts (Kiessling et al., 2023).

TABLE 1 Overview of studied plankton groups.

Plankton group	No. of extant species[1]	No. of extant fossilisable species[1]	Preservation[1]	Trophic mode[2]	Predictors of biogeography[3]
Planktonic foraminifera	50	50	Calcium carbonate (calcite) tests	Mixotrophic (symbionts) or heterotrophic	**SST**, strength of stratification, photo-synthetic biomass, ocean kinetic energy
Dinoflagellates	2000	260–320[a]	Organic-walled resting cysts	Autotrophic, mixotrophic or heterotrophic	**SST**, photosynthetic biomass, nutrient availability, strength of stratification
Coccolithophores	280	120	Calcium carbonate (calcite) plates	Mainly autotrophic, also mixotrophic (osmotrophic)	**SST**, **nutrient concentration**, light availability, strength of stratification

[a] Not all dinoflagellates are fossilisable, but about 13% to 16% of dinoflagellate species produce organic-walled resting cysts that are preserved in the sediment (Head, 1996).

[1] *Planktonic foraminifera*: Brummer and Kučera (2022); *Dinoflagellates*: Head (1996), Taylor et al. (2008); *Coccolithophores*: Young et al. (2005).

[2] *Planktonic foraminifera*: Schiebel and Hemleben (2017), Takagi et al. (2019); *Dinoflagellates*: Stoecker (1999), Jeong et al. (2005), Taylor et al. (2008); *Coccolithophores*: Godrijan et al. (2020, 2022).

[3] Main predictors are indicated in bold font. *Planktonic foraminifera*: Morey et al. (2005), Fenton et al. (2016), Rillo et al. (2021), Rufino et al. (2022); *Dinoflagellates*: Esper and Zonneveld (2002), Taylor et al. (2008), Chen, Irwin, and Finkel (2011), Hohmann et al. (2020); *Coccolithophores*: Mohan et al. (2008), Charalampopoulou et al. (2016), O'Brien et al. (2016), Benedetti et al. (2023).

Using time series of assemblage composition data since the LGM (past 24 kyr), we examine how planktonic foraminifera, dinoflagellates and coccolithophores responded to the environmental change during the last deglaciation—a climatic upheaval that is comparable to projected future anthropogenic global warming (Jackson & Overpeck, 2000). If the main predictor of the biogeography of these three plankton groups was temperature, their thermal niches remained static since the LGM (as shown for planktonic foraminifera: Antell et al., 2021; Waterson et al., 2017) and their capacity for range shifts remained unhindered because of high dispersal potential, all three groups should show a similar response to climate change. On the other hand, if the biogeography of any of the groups was strongly affected by biotic interactions or factors other than temperature change, their response to the warming could differ. For instance, Rillo et al. (2019) found no evidence for interspecific competition among extant planktonic foraminifera, but they mention the option that competition among other distantly related groups might be feasible and potentially explain the observed mismatch between fossil and modern observations. Furthermore, if evolutionary responses and adaptation in any of the groups would be faster, as hypothesized for coccolithophores (Bendif et al., 2023), the response to the warming of the last deglaciation could also differ among plankton groups.

2 | METHODS

2.1 | Data

The analyses are based on a previous compilation of 25 planktonic foraminifera assemblage time series (Strack et al., 2022) that, after an exhaustive search, has been expanded with 6 organic-walled dinoflagellate cyst (dinocyst) and 6 coccolithophore assemblage time series to compare patterns across groups (see Supporting Information Table S1 for full list of time series). Throughout this study, the terms 'assemblage' and 'community' are used as defined by Fauth et al. (1996), where 'community' refers to all species that occur in the same place at the same time, and 'assemblage' refers to all taxa of phylogenetically related groups within a community. Age information is presented throughout as kyr and ka (kyr referring to time periods and ka to a specific date; Aubry et al., 2009), with 0 ka denoting the 1950 Common Era. All assemblage time series were selected from records that were initially identified in public databases (e.g. pangaea.de), have available data for the entire assemblage (i.e. all individuals identified and counted), are located in the North Atlantic Ocean and adjacent seas, span the period from the LGM to the current warm period (i.e. past 24 kyr, but at least from 22.5 to 3.5 ka), and have sufficient temporal resolution to resolve millennial-scale climate events (i.e. average resolution of 0.57 kyr, ranging from 0.04 to 1.39 kyr). Some dinocysts species are affected by aerobic degradation in well-oxygenated waters (Zonneveld et al., 2007, 2008, 2019). However, we do not expect aerobic degradation to have a big influence on the composition of the dinocyst assemblages used here, because of the relatively high average sedimentation rates of 13 to 120 cm/kyr per dinocyst time series (see also Holzwarth et al., 2010).

All coccolithophore time series presented in this study are new and unpublished datasets because all initially identified published coccolithophore time series did not fit our selection criteria. Most of these identified coccolithophore time series either did not cover the entire time period of interest, were of too low a resolution, or did not provide sufficient information on the entire assemblage down to species level. Often species are lumped together by size (e.g. 'small Gephyrocapsa' or 'small placoliths') or by ecological preference (e.g. 'warm-water group'). These groups often do not contain the same species from site to site, but sometimes make a significant contribution to the assemblage. This made it impossible to harmonize the coccolithophore taxonomy to a satisfactory degree, leading us to reject most of the published data. Finally, we excluded one of the initially identified coccolithophore time series because it is known to be affected by dissolution, thus altering the species composition in these time periods, resulting in a total of 6 coccolithophore time series used in this study.

Although there are fewer dinocyst and coccolithophore time series than planktonic foraminifera time series, they also cover large parts of the latitudinal and thermal gradients in the North Atlantic Ocean (Figure 1). To ensure the chronological comparability of all analysed time series, we either used the revised age models included in the PALMOD 130k marine palaeoclimate data synthesis V1.1 (Jonkers et al., 2020) or we revised the published age models following the same approach as in Jonkers et al. (2020). Their age models are based on benthic foraminifera oxygen isotope data that have been manually calibrated to regional benthic foraminifera oxygen stacks (Lisiecki & Stern, 2016) as well as radiocarbon ages (see also Strack et al., 2022).

All plankton assemblage count data used here were taxonomically harmonized. Planktonic foraminifera assemblage data were harmonized following Siccha and Kucera (2017) (see Strack

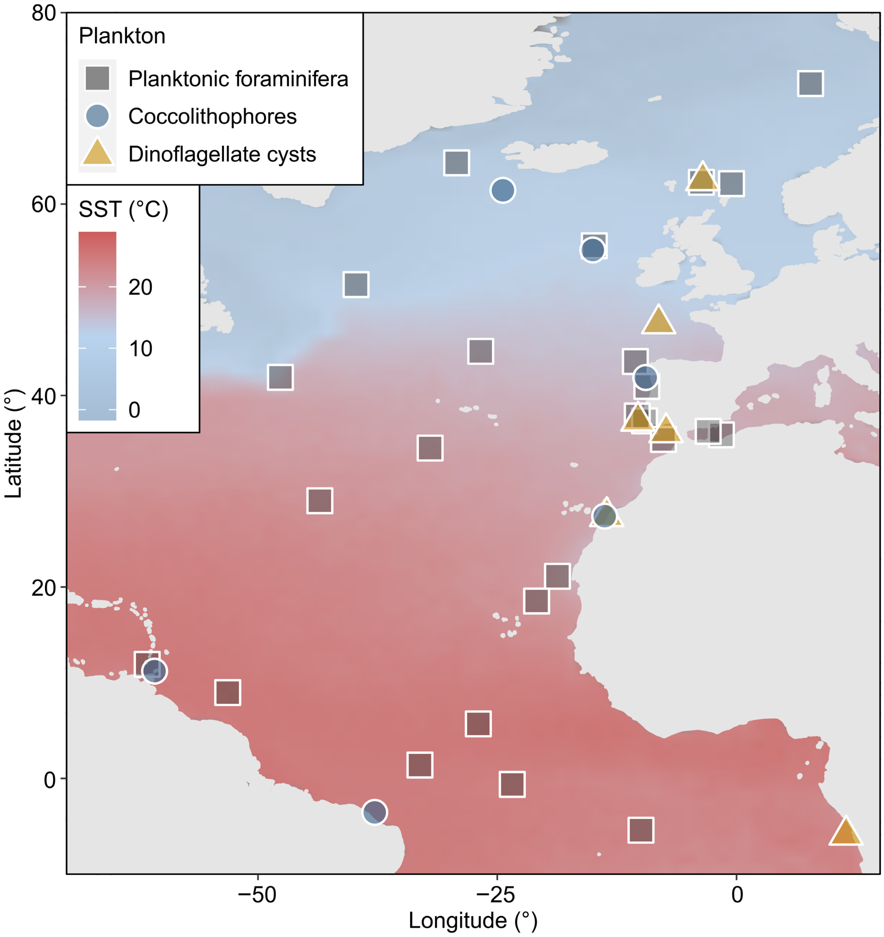

FIGURE 1 Location of microfossil assemblage data analysed including data on 25 planktonic foraminifera (grey squares), 6 dinocyst (yellow triangles) and 6 coccolithophore (blue circles) census count time series. Background colour gradient represents annual mean sea surface temperature (SST) from the World Ocean Atlas (WOA; Locarnini et al., 2019).

et al., 2022 for further details). Dinocyst taxonomy was harmonized following de Vernal et al. (2020) with minor additions following Zonneveld et al. (2013). Names that could not be resolved using synonym lists and assigned a harmonized name following de Vernal et al. (2020) and Zonneveld et al. (2013) were treated as unidentified specimens and excluded from assemblage analyses. These specimens were present in 4 time series and were rare taxa (relative abundances <3%). The protoperidinoids were also excluded from further assemblage analyses as this category includes all unidentified brownish cysts (de Vernal et al., 2020). Coccolithophore taxonomy follows Young et al. (2003), and coccoliths were counted using a scanning electron microscope (SEM) to ensure that all samples were resolved to species level (see Supporting Information for coccolithophore sample preparation). We merged *Coccolithus pelagicus* subspecies because they were not distinguished in all studies. Species not reported in the time series data were assumed to be absent (i.e. zero abundance), which is in accordance with the completeness of counts reported in the original studies. An average of 330 to 1250 planktonic foraminifera specimens, 200 to 550 dinocysts and 201 to 649 coccoliths were counted per sample and study, which are sufficient sample sizes to reliably determine relative abundances of each species (Al-Sabouni et al., 2007; Dennison & Hay, 1967; Phleger, 1960). The original data were given as either absolute or relative abundances, and after excluding unnecessary columns (unidentified or rare taxa that could not be harmonized), the abundances were recalculated to 100%. In total, 41 species of planktonic foraminifera, 53 species of organic-walled dinocysts and 34 species of coccolithophores were observed in our study (see Supporting Information Tables S2–S4 for full species lists).

2.2 | Principal component analysis on species composition

We applied a principal component analysis (PCA) on the harmonized assemblage data of each individual time series and extracted the first principal component (PC) axis (which explains most of the variance in the assemblage data) for each time series. Prior to conducting the PCA, the harmonized assemblage data were standardized and the variables were scaled to have a standard deviation of one and a mean of zero.

We acknowledge the site-specific nature of the PCA spaces, with each site having its unique PCA space based on the individual time series and recognize that the species contributing to the PCA axes may vary between sites within the same plankton group and between clades. This introduces potential challenges when directly comparing these spaces. However, we emphasize that the focus of this analysis is on evaluating the relative temporal pattern of compositional change and periods of significant compositional change rather than making direct quantitative comparisons. This approach mitigates potential issues arising from differences in the absolute scale or magnitude of individual PC spaces within and between individual clades.

2.3 | Generalized additive models on species composition

We used generalized additive models (GAMs) on the individual first PC axis scores to estimate the overall trend in each plankton clade. To do this, the fitted GAM predicts the overall first PC score from all sites in a single clade (i.e. plankton group) as a function of geological age. To ensure that all first PC axes were aligned in the same direction, we checked and, if necessary, changed their polarization by fitting linear models through all first PC axes. In total, the polarization of the first PC axes was changed (i.e. inverted) in 8 of the 25 planktonic foraminifera, 3 of the 6 dinoflagellate cyst and 2 of the 6 coccolithophore time series (Supporting Information Figure S1). This is a feasible approach as the sign of the PCA scores is arbitrary and doesn't carry any inherent meaning. We then interpolated the first PC scores in 0.5 kyr bins to account for differences in the resolution of the individual records. To prevent edge effects, we also restricted the interpolated data to the interval covered by all time series corresponding to plankton groups (i.e. 2.5–23 ka for planktonic foraminifera, 3.5–23 ka for dinocysts and 3.5–22.5 ka for coccolithophores). The advantage of using GAMs is that the complexity of the fitted model is determined objectively, as smoothing methods are applied automatically (Simpson, 2018). The significance of each GAM is given by associated *F*-statistics and tests of the null hypothesis of no trend, and uncertainties are estimated by 95% across-the-function confidence intervals.

Time periods of significant change are identified as periods where the confidence interval on the first derivative of the GAM-estimated trend does not include zero. Derivatives of the fitted trends are estimated using centred finite differences, and 95% across-the-function confidence intervals are calculated (see Simpson, 2018).

2.4 | Alternative GAM approach

Due to the site-specific nature of the PCA spaces and the potential challenges that may arise when directly comparing these spaces between different clades, we also considered an alternative GAM approach to validate our findings. This approach involves the calculation of temporal beta diversity for each site and running the GAM on these values (see Supporting Information for a more detailed explanation of this approach). As the alternative approach showed similar results (see Supporting Information Figures S2–S4), we conclude that our PCA/GAM analysis is a valid approach to investigate the relative temporal patterns and periods of significant compositional change between different plankton groups.

2.5 | Sensitivity analysis

We conducted a sensitivity analysis to check whether our observed plankton signals might be the result of sampling bias, as the number of available time series for planktonic foraminifera is about four times higher than the number of available time series for dinocysts and coccolithophores. To do this, we resampled the planktonic foraminifera dataset and created two subsets. One subset with time series closest (geodesic distance) to the dinocyst time series and another subset with time series closest to the coccolithophore time series. We then recalculated the overall trend (GAMs) and periods of significant change (1st derivative of GAMs) for these two planktonic foraminifera subsets. The significance of the GAMs of these subsets is also given by associated F-statistics and tests of the null hypothesis of no trend.

2.6 | Spatio-temporal biodiversity change

To evaluate the spatio-temporal pattern of local biodiversity change, we followed the analysis of Strack et al. (2022). For each location and time step, we calculated species richness and the proportion of gained and lost species compared to the oldest sample in the time series, that is, the LGM. Species gains and losses take into account species identity (Antão et al., 2020) and were calculated for each sample in a time series as the proportion of species either gained or lost in comparison to the oldest sample in the time series. This proportion was calculated in relation to the total number of species observed in both samples pooled together (i.e. the oldest sample and the analysed sample).

In addition to Strack et al. (2022), we also described the diversity of assemblages, but by calculating the effective number of species (ENS; MacArthur, 1965) as the exponential of the abundance-based Shannon entropy (Shannon, 1948):

$$\mathrm{ENS} = \exp\left(- \sum_{i=1}^{S} p_i \times \ln p_i \right),$$

where S is the number of species at a specific site and p_i is the relative abundance of the ith species.

Rates of local plankton biodiversity change were then expressed as the slopes of linear models for species richness, gains, losses and ENS across the entire studied time interval examined for each time series. It is important to note that when expressed in this way, the slopes only approximate the overall amount of change across time, and the underlying change may not have been monotonic. In this approximation, negative trends in certain parameters indicate that younger samples in the time series are less different from the baseline (the oldest sample in the time series) than the older samples. Positive trends indicate that younger samples in the time series are more different from the baseline than the older samples (see Extended Data Figures 3 and 4 and Methods of Strack et al. (2022) for a more detailed explanation).

To better understand the spatio-temporal dynamics of local plankton biodiversity, we further assessed the difference between the species richness and ENS of each sample in a time series and the mean LGM species richness and ENS of that time series. Mean LGM species richness and ENS were determined for all samples falling within the LGM interval (i.e. 19–23 ka, as defined in Mix et al. [2001] and Kucera, Rosell-Melé, et al. [2005]). These differences were then gridded into Hovmoller-like plots with a grid cell resolution in time and space of 1 kyr and 2.5°.

2.7 | R packages

All statistical analyses were performed in R version 4.3.3 (R Core Team, 2024) using the 'tidyverse' package (Wickham et al., 2019), 'janitor' package (Firke, 2023) and 'ncdf4' package (Pierce, 2023) for cleaning and importing the data; 'codyn' (Hallett et al., 2016, 2020) and 'vegan' (Oksanen et al., 2020) packages for community structure analyses; 'FactoMineR' (Lê et al., 2008) and 'factoextra' (Kassambara & Mundt, 2020) for the PCA; 'gratia' (Simpson, 2024) and 'mgcv' (Wood, 2011, 2017) for the GAM analysis; 'geosphere' (Hijmans, 2022) for spherical trigonometry used in the sensitivity analysis; and 'ggplot2' (Wickham, 2016), 'raster' (Hijmans, 2023) and 'patchwork' (Pedersen, 2024) for the plots.

3 | RESULTS

We analysed 25 planktonic foraminifera, 6 dinocyst and 6 coccolithophore assemblage time series across the latitudinal gradient of the North Atlantic Ocean (Figure 1, Supporting Information Table S1). In all three plankton groups, the first PC axes of compositional change show a unidirectional trend, with the first PC axes of individual trends explaining 20%–65% of the variance in planktonic foraminifera, 13%–23% in dinocyst and 17%–31% in coccolithophore time series (Figure 2). The GAMs indicate that the overall temporal pattern of all three plankton groups is characterized by a unidirectional and statistically significant trend in compositional change (Table 2 and Figure 3a). However, it is important to note that these trends are averaged per plankton group (i.e. GAMs) and individual time series may show distinct deviations from the GAM trends (Figure 2), reflecting local changes at each of the sites analysed. While the periods of significant change are similar for planktonic foraminifera and dinocysts, the timing is different for coccolithophores. For planktonic foraminifera and dinocysts, the shift in assemblage composition started approximately with the onset of global warming (15.5–17 ka ago), and the assemblages continued to change throughout the Holocene until at least 5 ka ago (Figure 3). Interestingly, coccolithophore assemblages appear to have changed at a constant rate throughout the past 24 kyr, irrespective of the prevailing temperature change. All three plankton groups show a substantial degree of continued assemblage change even during the current warm period, when global temperature change was low (Figure 3; see also Strack et al. [2022] for more detailed analyses of planktonic foraminifera).

Because of the uneven sampling of the three plankton groups, we tested whether the overall trend of planktonic foraminifera (the group with the most time series) is similar when subsampling to the time series closest to the dinocyst and coccolithophore time series

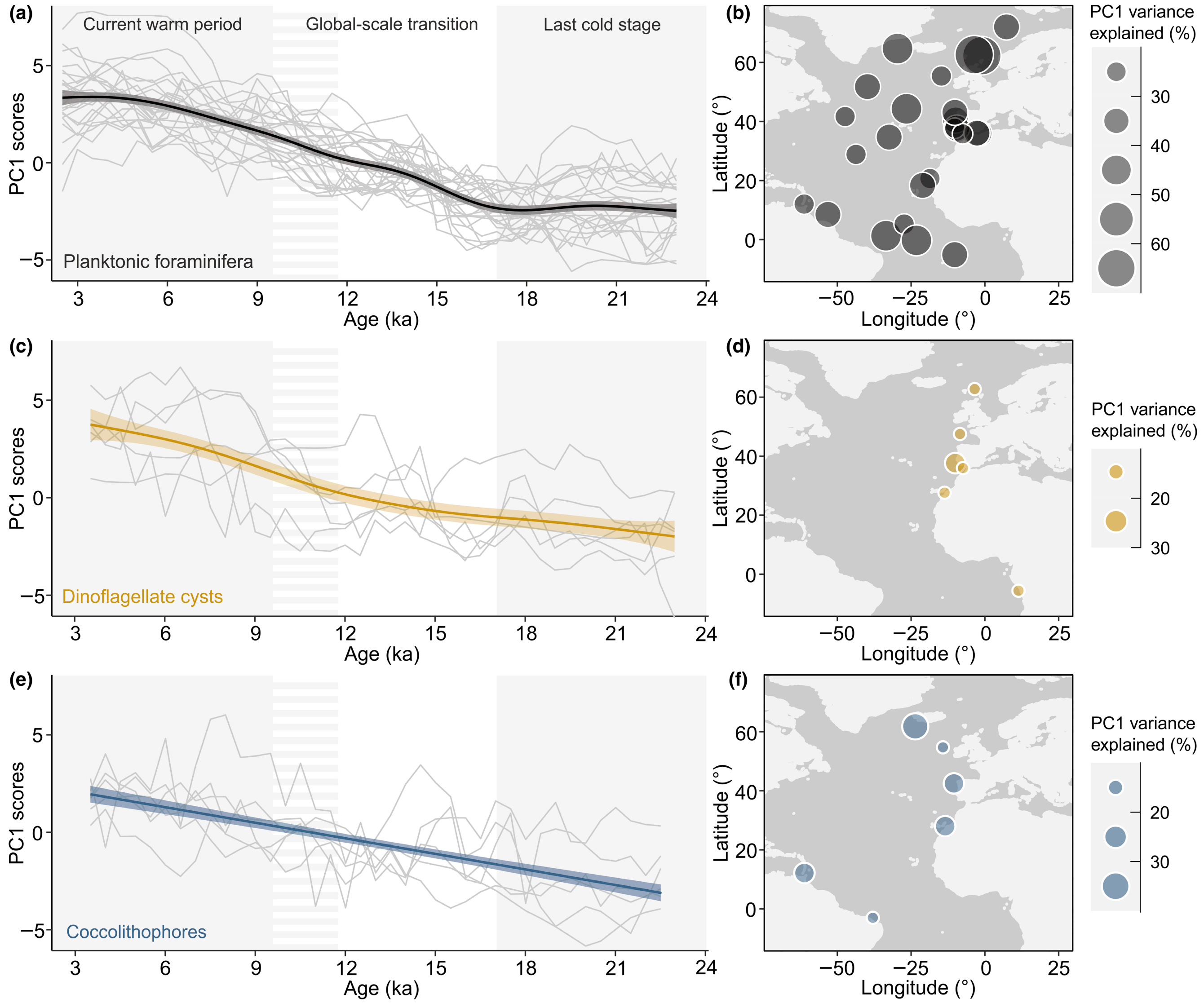

FIGURE 2 Compositional change in marine plankton groups during the past 24,000 years obtained from analysis of time series of census counts of three plankton groups: planktonic foraminifera (a,b, dark grey), dinocysts (c,d, yellow) and coccolithophores (e,f, blue). (a,c,e) Compositional change within each time series, visualized as first principal component (PC1) axis scores (grey lines, interpolated at 0.5 kyr). Overall compositional change is shown as generalized additive model (GAM) fits (coloured lines) and their 95% confidence intervals (coloured shading). (b,d,f) Amount of variance explained by each individual PC1 axis at the location of each time series. The grey striped area in panels a, c, e represents the period from the beginning of the Holocene (11.7 ka ago) until the stabilization of the global temperature (9.5 ka ago; see also Figure 3b).

TABLE 2 Summary statistics of fitted generalized additive models (GAMs) on first PCs by plankton group with associated *F*-statistic and test of the null hypothesis of no trend (*p* value).

Dataset	*R*-sq. (adj)	*n*_sample	edf	*F*	*p* value
Planktonic foraminifera (*n* = 25)	0.729	1050	8.173	344.9	<<0.0001
Dinoflagellate cyst (*n* = 6)	0.496	240	3.503	66.69	<<0.0001
Coccolithophore (*n* = 6)	0.437	234	1	181.9	<<0.0001
Planktonic foraminifera subset I (*n* = 6)	0.642	252	6.606	67.56	<<0.0001
Planktonic foraminifera subset II (*n* = 6)	0.708	252	4.69	129.2	<<0.0001

Note: *R*-sq. (adj): adjusted *R*-squared for the model; *n*_sample: number of data points (samples); edf: estimated degrees of freedom; *n*: number of time series. Planktonic foraminifera subsets I and II relate to the sensitivity analysis described in the Methods and Figure 4.

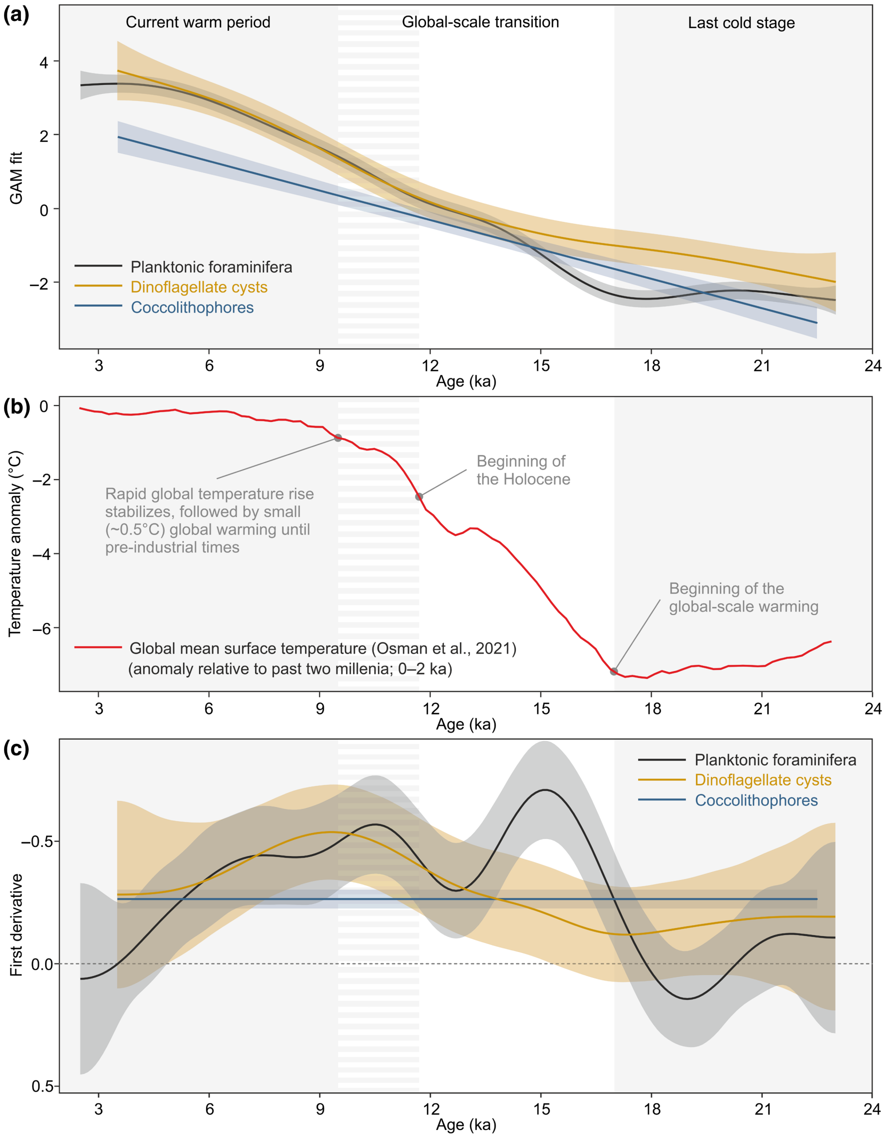

FIGURE 3 Relationship between marine plankton assemblage and global warming during the past 24,000 years. (a) Overall compositional change shown as generalized additive model (GAM) fits (see also Figure 2) for planktonic foraminifera (dark grey), coccolithophores (blue) and dinocysts (yellow) and their 95% confidence intervals (coloured shading). (b) Evolution of the global mean surface temperature (Osman et al., 2021; red line). The temperature anomaly is referenced to the past two millennia (0–2 ka). (c) First derivatives of the GAM estimated trends and their 95% confidence intervals (coloured shading).

(6 sites each). This sensitivity analysis shows that the overall trend and the period of significant compositional change in planktonic foraminifera are robust to sampling bias (Figure 4 and Table 2).

To determine how these temporal patterns apply to the individual components of assemblage change, we next compared changes in alpha-diversity and species gains and losses by comparing the slopes of linear models (Figure 5 and Supporting Information Figures S5 and S6 for the two data subsets used in the sensitivity analysis). It is important to note that in this approximation the underlying changes may not have been monotonic (see Methods section for further details on interpreting the trends). This analysis revealed that for all three plankton groups, the largest change in species richness (and effective number of species) occurred in the mid-latitudes, while the equatorial region remained relatively stable or showed a slight decrease in species richness (Figure 5a,g). All plankton groups show an asymmetry in species gains and losses, with the magnitude of local immigration being higher than local extinction (Figure 5c–f). We observe a higher accumulation of gained, new species in the mid-latitudes (Figure 5c) and relatively stable values in the equatorial region, consistent with the local trends in richness. In contrast, species losses were highest in the equatorial region, but exhibited a lower magnitude than species gains in the mid-latitudes (Figure 5e). We also see a decrease in the proportion of lost species in the mid-latitudes over the past 24 kyr (Figure 5e), implying that most species present in this region during the LGM persisted throughout the deglaciation, but the community was progressively enriched by colonization from lower latitudes. Finally, we observe a consistent decrease in ENS in the equatorial time series for all plankton groups over the past 24 kyr (Figure 5g), even though the change in species richness in the equatorial region was comparably small (Figure 5a), meaning that most species present in the lower latitudes during the LGM remained, but the dominance structure of species in these assemblages changed over time. The median values of species richness, gains and losses are comparable between the different plankton groups (Figure 5b,d,f). In contrast,

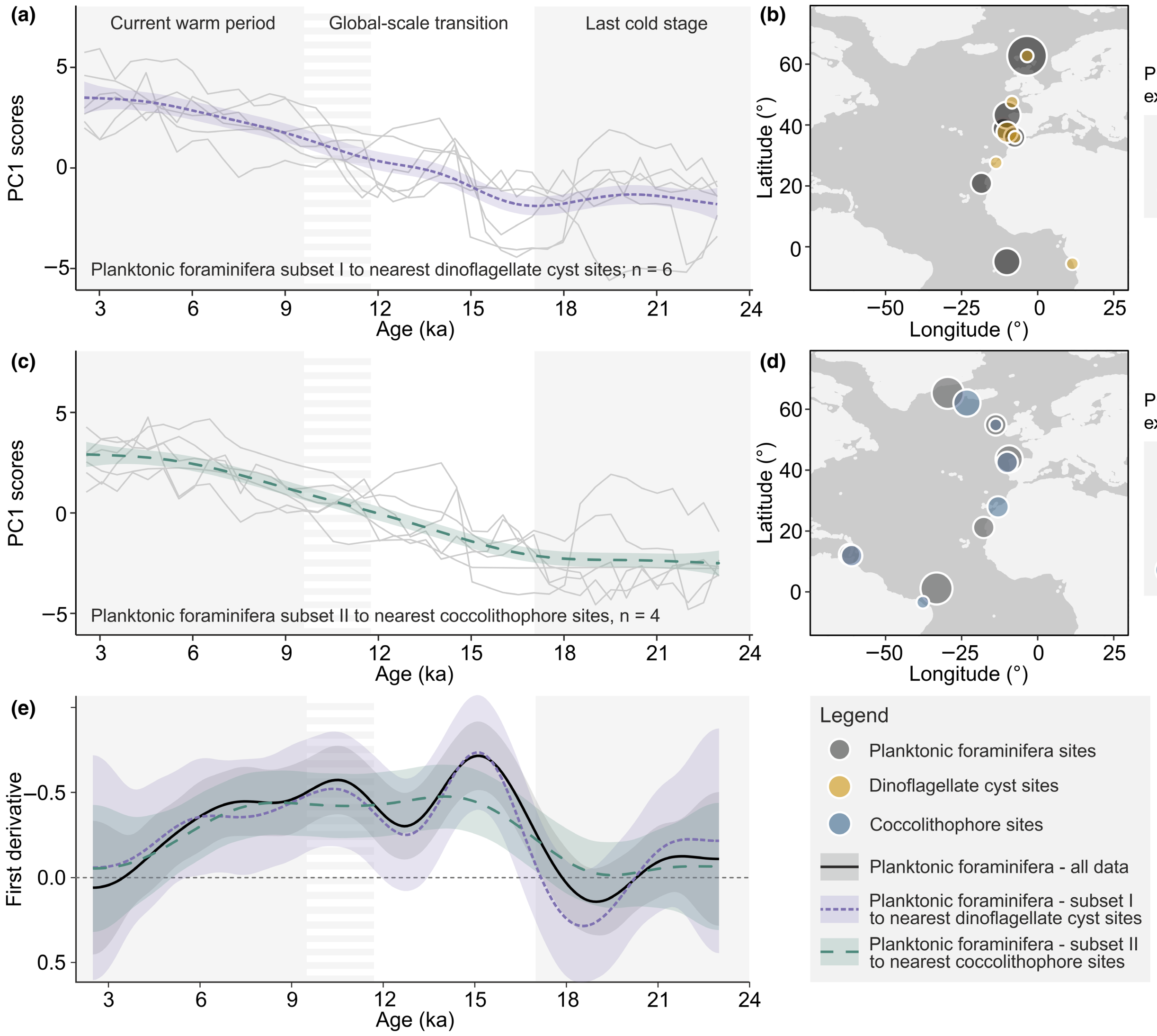

FIGURE 4 To check for sampling bias, the planktonic foraminifera dataset (Figure 2a,b) was resampled to include only the time series closest to the dinocyst (a,b, subset I) and the coccolithophore (c,d, subset II) records. (a,c) Compositional change within individual time series shown as first principal component (PC1) axis scores (grey lines, interpolated at 0.5 kyr) and overall compositional change shown as generalized additive model (GAM) fits (coloured lines) and their 95% confidence intervals (coloured shading). (b,d) Variance explained by individual PC1 axes at each site. (e) First derivatives of the GAM estimated trends and their 95% confidence intervals (coloured shading).

the median ENS of dinocysts appears different when compared to planktonic foraminifera and coccolithophores (Figure 5h), probably due to the relatively high spatial ENS variability in the dinocyst time series analysed (Figure 5g).

The spatio-temporal analysis of biodiversity changes in the three plankton groups revealed that the notable increase in species richness in the mid-latitudes started to accumulate during the last deglaciation around 15 ka (Figure 6). The observed decrease in equatorial ENS (Figure 5g) started with the onset of the current warm period around 12 ka for planktonic foraminifera and dinocysts, and even with the onset of global warming around 18 ka for coccolithophores, and has intensified towards the present (Figure 6). Interestingly, species richness and ENS of dinocysts and coccolithophores appear to peak in the mid-latitudes between 6 and 9 ka ago, followed by a steady decrease (Figure 6d–i). A similar peak in alpha-diversity is not as clearly discernible in the planktonic foraminifera time series, where we have more records in the mid-latitudes (Figure 6a–c).

4 | DISCUSSION

The key focus of this study is the comparison of the relationship of additional plankton groups (i.e. dinoflagellates and coccolithophores) to climate change over the past 24 kyr with previously established trends in planktonic foraminifera (Strack et al., 2022). The joint analyses of the assemblage composition time series of these three plankton groups reveal that the transformation of the marine environment associated with global warming during the last deglaciation was accompanied by a significant change in marine plankton assemblages. Despite the large differences in sampling, species diversity

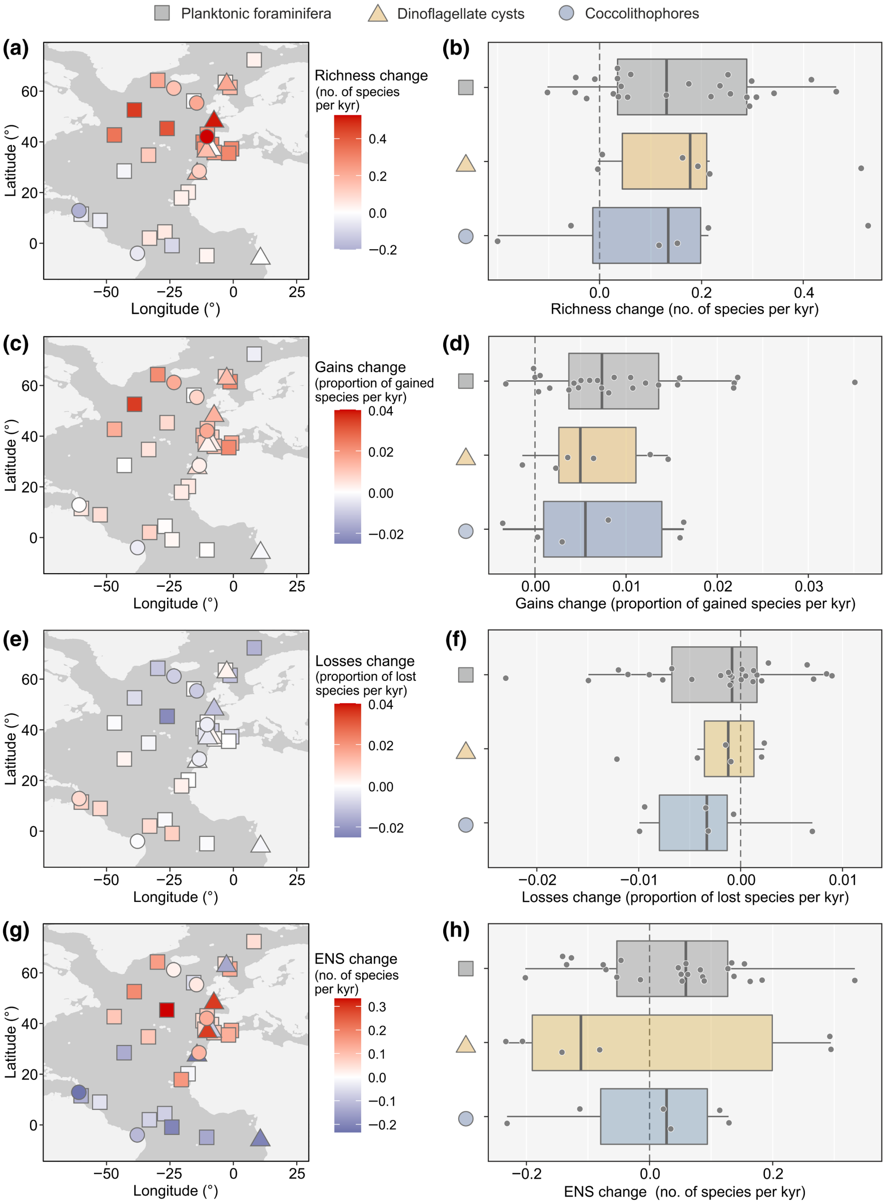

FIGURE 5 Local rates of change in marine plankton biodiversity during the past 24,000 years. Spatial distribution of rates of change in (a,b) species richness, the proportion of (c,d) species gained and (e,f) species lost, and (g,h) effective number of species (ENS) since the Last Glacial Maximum for planktonic foraminifera (grey squares), dinocysts (yellow triangles) and coccolithophores (blue circles). The rate of change is quantified for each time series as the slope of a fitted linear model (see Methods, and Extended Data Figures 3 and 4 of Strack et al., 2022). For example, a positive slope of the change in richness (or ENS) indicates a net increase in species number (or ENS) over time, a positive change in gains indicates an accumulation of new species over time and a positive change in losses indicates an accumulation of species losses over time. The lower and upper hinges of the box plots correspond to the 25th and 75th percentiles, and the median is indicated by the thick grey vertical lines. The lower and upper whiskers are constrained within the 1.5*IQR (interquartile range). Dashed vertical lines in the box plots indicate zero; note the different x-axis scales of the box plots.

and ecology of planktonic foraminifera, dinoflagellates and coccolithophores, these three plankton groups show remarkably similar overall trends in the rates and spatio-temporal dynamics of local biodiversity change over the past 24 kyr (Figures 5 and 6, Supporting Information Figures S5 and S6). While they show a non-linear relationship with temperature during climatically more stable periods (Figure 3a,b), they also show some distinct differences between clades in the detailed temporal pattern and periods of significant compositional change (Figure 3c). Our sensitivity analysis (Figure 4) indicates that the observed similarities and differences among the patterns of the different clades are not affected by (latitudinal) sampling bias, even though the number of dinocyst and coccolithophore time series included is four times lower than the number of planktonic foraminifera time series included, and the dinocyst and coccolithophore time series have a smaller spatial coverage (Figure 1, Supporting Information Figure S7). The variance explained by the first PC axes differs between sites and plankton groups, following a general trend of decreasing explained variance with increasing species richness in the assemblages (Supporting Information Figure S8). Regardless of the site-specific nature of the PCA space, the observed non-linear relationship of the different clades with temperature is considered robust, as confirmed by an alternative methodological approach (see Supporting Information and Figures S2–S4).

4.1 | Similarities in the local rates of biodiversity change during the past 24 kyr

In all three groups, the change associated with deglacial warming is characterized by a distinct, long-lasting shift in the species composition of plankton assemblages (Figure 3), reflecting the dominance of poleward species migration leading to an asymmetry between local immigration and extinction (Figure 5c–f) and an accumulation of species in the mid-latitudes starting at around 15 ka

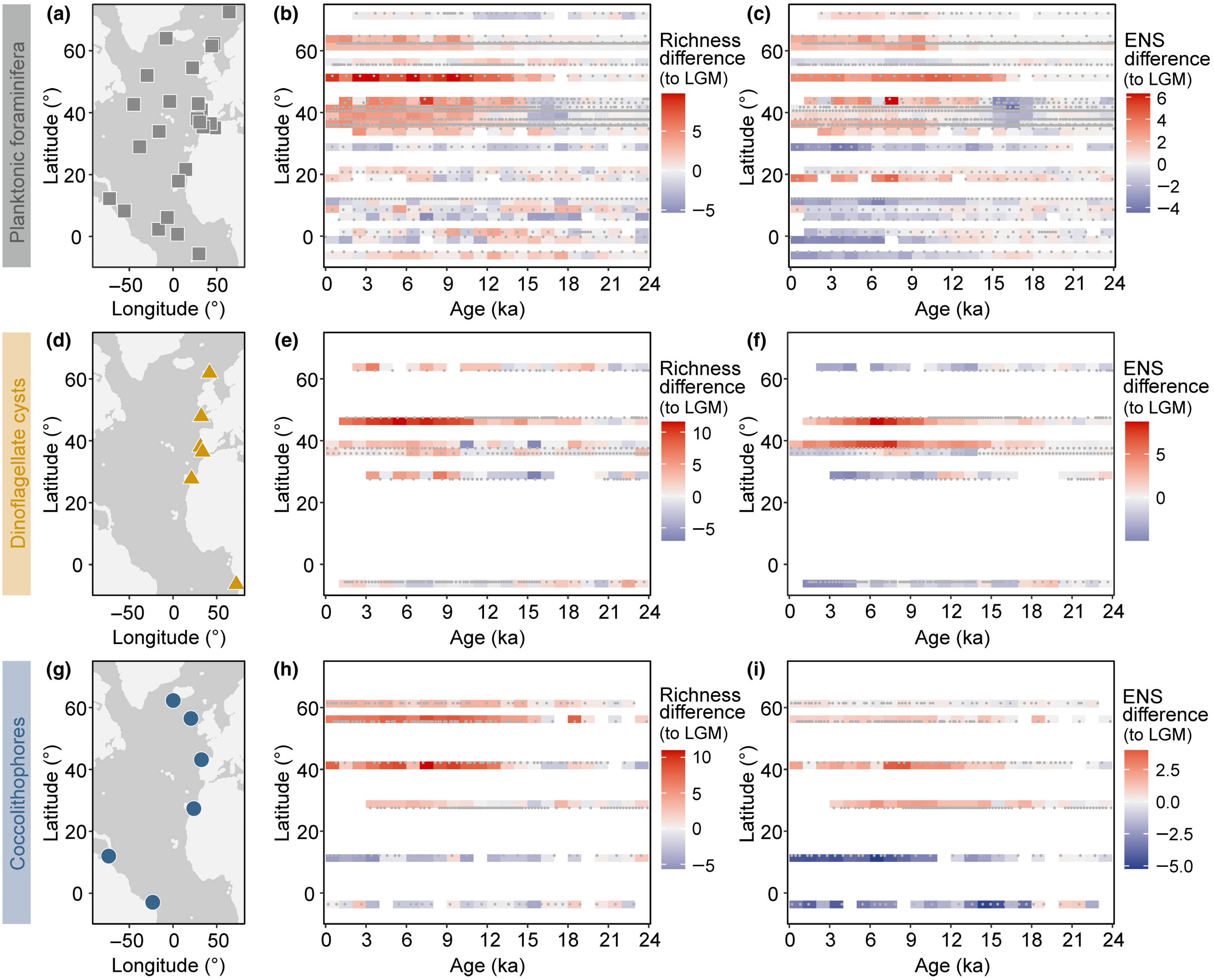

FIGURE 6 Spatio-temporal evolution of species alpha-diversity during the past 24,000 years. (a,d,g) Locations of individual time series per plankton group: planktonic foraminifera (grey squares), dinocysts (yellow triangles) and coccolithophores (blue circles). Differences in (b,e,h) species richness and (c,f,i) effective number of species (ENS) between each given sample and the Last Glacial Maximum (LGM) mean (i.e. 19–23 ka) of each time series. Grid cells show the mean difference of the given samples with a resolution of 1 kyr by 2.5° latitude. Positive numbers (reddish colours) indicate that species richness or ENS has increased since the LGM, and negative numbers (blueish colours) indicate that species richness or ENS has decreased since the LGM. Grey dots within the grids represent each individual sample.

(Figures 5a and 6). Although species richness remained relatively stable in the lower latitudes during the past 24 kyr (Figures 5a and 6b,e,h), there is a consistent decrease in ENS in the equatorial time series during the Holocene (Figure 6c,f,i). Thus, even though there were few or no local species extinctions after the deglaciation, some equatorial species became more dominant, resulting in less diverse (lower ENS) assemblages. The observed decrease in lower latitude ENS may therefore suggest that some equatorial plankton species have already reached the maximum of their thermal range in the Holocene, rendering equatorial plankton biodiversity vulnerable to continued global warming. Indeed, recent losses in tropical species richness have been described for many pelagic and benthic chordates and benthic invertebrates such as gastropods, bivalves and arthropods (Chaudhary et al., 2021), and are predicted for reef corals (Kiessling et al., 2012), planktonic foraminifera (Yasuhara, Wei, et al., 2020) and marine species in general (Brown et al., 2022; Hodapp et al., 2023). In a recent deep-time analysis of the fossil record of planktonic foraminifera, Woodhouse et al. (2023) revealed a global, clade-wide shift of planktonic foraminifera towards the equator over the past 8 Myr in response to the cooling of the Earth related to ice sheet formation and the associated emergence of new (vertical) niches at lower latitudes due to colder bottom waters from high latitudes (Fenton et al., 2023). About 8 Ma ago—a time period when the average global temperature was as high as that predicted for future anthropogenic global warming by the end of this century—tropical species lived over 3000 km from the equator. This long-term, clade-wide shift of the plankton likely has different underlying mechanisms and lacks the glacial–interglacial dynamics we observe in this study, which are likely periodic, but the pattern is similar. So, the observed decrease in ENS at lower latitudes during the Holocene (Figure 6) may be an early indicator of a plankton shift away from the equator. Thus, our findings render the prediction more likely that current and future anthropogenic warming of the oceans may lead to an intensification of the reshuffling of marine flora and fauna, potentially leading to a decline (and possibly extinction) of both endemic polar and equatorial species (Yasuhara & Deutsch, 2022).

4.2 | Similarities in the non-linear relationship to temperature during the past 24 kyr

All three plankton groups show a pronounced non-linear relationship with climate change that is mainly evident from the continued compositional change into the Holocene despite a more subdued temperature change (Figure 3). Assemblages of planktonic foraminifera and dinoflagellates continued to change until around 5 ka, while coccolithophore assemblages changed at the same rate throughout the whole investigated time period, despite the fact that the rate of global warming changed at the start of the current warm period (around 11 ka, Figure 3b). The observed continued change in dinoflagellate and coccolithophore assemblages during the Holocene shows that previous findings for planktonic foraminifera (Strack et al., 2022) are not group-specific, but occur in clades with different diversities, trophic strategies and overall ecology.

The non-linear relationship of all investigated plankton groups with temperature change during the past 24 kyr suggests either that other environmental drivers with different effect strengths and different temporal evolution during the past 24 kyr have affected the plankton, or that the relationship of plankton assemblages with temperature change is modulated by biotic interactions or other processes (such as extinction debt, neutral drift or adaptation). As detailed in Strack et al. (2022), extinction lag and neutral drift seem unlikely to be the main drivers of the continued compositional change of planktonic foraminifera during the Holocene. Long extinction lags (of several thousand years) were considered unlikely for marine plankton due to their short life cycle and high dispersal potential by currents. Also, the accumulation of species in the mid-latitudes after the end of the last deglaciation is not a short transient phenomenon but persists for several millennia (Figure 6), and we do not observe a continuous loss of species in the mid-latitudes during the middle to late Holocene that would indicate an extinction 'payoff' within the time interval studied (Figure S9). The documentation of a rapid change in planktonic foraminifera assemblages during a short-lived cold interval (Heinrich Event I, Broecker, 1994; Figure 6b,c and Strack et al., 2022) further suggests that any lags in plankton assemblage change related to climate change are likely shorter than a millennium. The overall trends in the rates and spatio-temporal dynamics of local biodiversity change (e.g. poleward species migration, decline of equatorial ENS) are consistent among the investigated plankton groups (Figures 5 and 6), indicating that underlying selective processes are more likely than purely stochastic processes (neutral drift) as a cause for these similarities. Instead, it has been suggested that the continued compositional change may indicate a shift in the dominant drivers of plankton assemblage change from more abiotic-dominated causes (i.e. environmental drivers) during the last deglaciation to more biotic-dominated causes in the Holocene (Strack et al., 2022).

4.3 | Assemblage change differences among plankton groups and potential explanations

Incorporating the new results for dinoflagellates and coccolithophores from this study, it can be concluded that while the non-linear relationship with temperature change is recognized in all three plankton groups, there are also noteworthy differences in the overall trend of coccolithophores compared to the other two clades. Planktonic foraminifera and dinoflagellate species assemblages began to change on average at the same time as global warming, suggesting a potential direct response to this temperature change. In contrast, average coccolithophore species assemblages changed at a constant rate during the investigated time period (Figure 3b,c), indicating that the drivers of community assembly may vary among clades.

Even though sea surface temperature (SST) is thought to be the main predictor of the distribution and diversity of the plankton groups investigated (see Table 1; Charalampopoulou et al., 2016; Chen, Irwin, & Finkel, 2011; Esper & Zonneveld, 2002; Fenton et al., 2016; Morey et al., 2005; O'Brien et al., 2016; Rillo et al., 2021; Rutherford et al., 1999; Taylor et al., 2008), it is not the sole environmental driver (e.g. Benedetti et al., 2023; Hohmann et al., 2020; Rillo et al., 2021). We assume that the large temperature change during the last deglaciation overwhelmed other (environmental) processes during this period. Nevertheless, other abiotic factors may also be driving changes in plankton biogeography, especially at lower latitudes (Rillo et al., 2021) and during periods of lower temperature change compared to the deglaciation. For instance, insolation changes during the current warm period have led to a reduced seasonal temperature range and water column stratification in the mid to late Holocene (Berger & Loutre, 1991; Solignac et al., 2006). These changes may influence plankton biogeography and diversity to a different degree, with some plankton clades being more sensitive or responsive due to their distinct ecologies. For example, a lower seasonal temperature range could favour the expansion of warm-adapted species, while changes in water column stratification and associated changes in nutrient availability and light penetration could impact the distribution of species adapted to various (vertical) ecological niches.

Furthermore, Benedetti et al. (2023) used a modelling framework to assess the importance of several environmental factors on plankton distribution. They found nutrient concentration (i.e. the excess of nitrate over phosphate) to be more important than SST for coccolithophore species distribution, while SST was the main predictor of the species distribution of all other plankton groups (except pteropods). This disparity may further explain the divergent assemblage changes observed in coccolithophores compared to dinoflagellates and planktonic foraminifera. It is also important to note that in our analysis we compared overall compositional change to a single global driver (mean SST), but this change at the clade level, as indicated by the GAM fit, is the result of local drivers at the regional scale rather than global drivers. At the regional scale, it is noticeable that in the lower latitudes, coccolithophores show an early response to the last deglaciation, marked by a distinct decrease in ENS with the onset of the global warming at around 18 ka, whereas this occurred later (between 12 and 15 ka) in dinoflagellates and planktonic foraminifera (Figure 6). This may indicate that some coccolithophore species have already reached the maximum of their thermal range with the onset of the last deglaciation. Considering the diversity of trophic strategies and ecologies of the investigated plankton groups, these results suggest that the vulnerability to future equatorial warming may vary among different plankton groups, with phytoplankton groups potentially being at higher risk. Finally, the constant compositional change of coccolithophores may also hint towards a more important role of adaptation in the relationship of coccolithophores to global warming compared to the other investigated plankton clades. This interpretation is consistent with rapid diversification events in a cosmopolitan coccolithophore species within the past 140 kyr, with the most recent events occurring during the last glacial cycle (Bendif et al., 2023). This constant adaptability of coccolithophores may suggest an inherent capacity to adapt to evolving environmental conditions. Either way, the apparent differences in response times and drivers among coccolithophores, dinoflagellates and planktonic foraminifera highlight the multifaceted nature of their relationship to environmental change and emphasize the urgent need for targeted research into the adaptive capacity of other plankton groups and the influence of additional environmental factors, which will be crucial in predicting the fate of planktonic communities under future anthropogenic warming.

Furthermore, biotic factors, such as ecological interactions, also drive compositional change of assemblages and have an important effect on plankton community structure (Lima-Mendez et al., 2015). The poleward migration of species to new habitats (Strack et al., 2022) and the persistence of the original species in these habitats (Figure 6) caused the formation of novel assemblages after the last deglaciation (Strack et al., 2022), in which new direct and indirect interspecific ecological interactions are likely to have emerged. For the investigated plankton groups in particular, these could include changes in grazing pressure (all groups), changes in food availability (planktonic foraminifera as well as some dinoflagellates and coccolithophores are mixo- or heterotroph), changes in endosymbiont fitness (algal endosymbiont-bearing planktonic foraminifera and dinoflagellates) and exposure to new pathogens and/or parasites (all groups). Such novel ecological interactions would cause pressure on all groups and potentially drive assemblage change and local adaptation (Brockhurst et al., 2014; Liow et al., 2011).

In conclusion, the non-linear relationship of all investigated plankton groups with temperature change and the observed prolonged plankton compositional change into the Holocene (Figure 3c) may indeed indicate a shift in the dominant drivers of plankton assemblage change from more abiotic-dominated causes (temperature forcing) during the last deglaciation to more biotic-dominated causes. A similar shift in the dominant driver of assemblage change was found in a 24 kyr record of terrestrial plants by Doncaster et al. (2023). They found that abiotic forcing (temperature) was the main driver of community assembly until around 9 ka ago, while internal processes (such as competitive and facilitative interactions among species) dominated community assembly until the present, highlighting the importance of biotic interactions and mechanisms during more climatically stable periods.

Applying these findings to our study, the reduced temperature change, species migration and resulting novel ecological interactions likely led to a large-scale readjustment of the plankton community to warmer conditions after the onset of the current warm period. These novel ecological interactions may potentially be a consequence of environmental change during the last deglaciation, suggesting an indirect link to the preceding climatic shift. In this hypothesis, the plankton response to a large, unidirectional climate change would involve a cascade of direct responses through asymmetric range shifts leading to the establishment of novel communities and interactions, followed by subsequent community transformation under reduced environmental change due to biotic interactions in the new communities. Furthermore, the differences in the overall response of coccolithophores compared to planktonic foraminifera and dinoflagellates highlight the intricate interplay of environmental drivers, biotic interactions and adaptation that shape marine plankton communities.

Our study provides insights into the potential historical shift from more abiotic- to more biotic-dominated causes of changes in plankton assemblages during the past 24 kyr. It is unclear whether these trends persist today or how they will evolve under predicted future anthropogenic warming. If similar dynamics are at play during current climate warming, we can investigate the ongoing interplay of abiotic and biotic drivers by examining the current domain of plankton communities. This information, combined with data from sedimentary archives, could then be used to determine whether future changes in marine plankton will be governed by similar patterns and whether novel dynamics will emerge. This approach could help formulate more accurate predictions of the future response of the marine ecosystem to predicted anthropogenic warming.

5 | CONCLUSION

The objective of this study was to reveal the spatio-temporal biodiversity patterns of planktonic foraminifera, dinoflagellates, and coccolithophores in the North Atlantic Ocean over the past 24 kyr. The following conclusions can be drawn from our data:

1. The last deglaciation significantly affected both zoo- and phytoplankton assemblages. Despite differences in the ecology, diversity and number of time series analysed among the investigated plankton groups, they show remarkably similar trends

in the rates and spatio-temporal dynamics of local biodiversity change during the past 24 kyr.

2. All plankton groups show a pronounced non-linear relationship with climate change marked by continued compositional change into the Holocene, despite low temperature changes, until at least 5 ka, that is, several millennia after the end of the last deglaciation and rapid global warming (see also Strack et al., 2022). The most likely explanation for the continued assemblage change during the climatically stable Holocene is a shift in the dominant drivers of plankton assemblage change from more abiotic-dominated causes during the last deglaciation to more biotic-dominated causes with the onset of the Holocene.
3. Throughout the past 24 kyr, coccolithophores have exhibited a consistent rate of overall compositional change, seemingly regardless of prevailing temperature change. This suggests that the importance of other (environmental) drivers and/or adaptation processes may vary among clades.

In conclusion, our comprehensive analysis of planktonic foraminifera, dinoflagellates and coccolithophores over the past 24 kyr shows that zoo- and phytoplankton were affected by the last deglaciation, which is in its magnitude of warming comparable to future projected global warming (Jackson & Overpeck, 2000). The nuanced responses and disparities among these vital groups with varying ecologies underscore the intricate interplay of environmental drivers, biotic interactions and adaptation shaping marine plankton communities during the past 24 kyr. We therefore advocate for multi-faceted approaches that consider various plankton groups and trophic levels, diverse environmental parameters, biological interactions and group-specific rates of adaptation when assessing the impacts of ongoing and future anthropogenic climate change on the marine ecosystem. Also, most of the environmental change that has occurred over the past 24 kyr has taken at least 6000 years to occur, whereas anthropogenic global warming is expected to occur over a much shorter time period. Furthermore, cold-adapted species were confronted with warm conditions after the last deglaciation, whereas warm-adapted species will face even warmer conditions in the future. Although this study reveals how the plankton community has responded to environmental change similar in magnitude to projected future anthropogenic warming, the question remains whether plankton communities will cope in a similar way with more rapid global warming. This is particularly important given the potentially significant role of biotic interactions in the observed response cascade.

AUTHOR CONTRIBUTIONS

H.H. and M.K. conceived the project idea, and all authors jointly contributed to the design and planning of the project. T.S. conducted the data analyses and designed the figures. T.S. wrote the R code with contributions from L.J. as well as M.C.R.; and K.-H.B. conducted the coccolithophore assemblage counts. All authors interpreted and discussed the results, and contributed to the writing and editing of the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

All data used and analysed during the current study are publicly available in the PANGAEA and NOAA National Centers for Environmental Information repositories. For information on links and paper references to individual assemblage datasets, see Supporting Information Table S1. The coccolithophore assemblage data from this study are available at PANGAEA (https://doi.org/10.1594/PANGAEA.965722). Modern global mean surface temperature and globally resolved surface temperature since the LGM are available at NOAA (https://www.ncei.noaa.gov/access/world-ocean-atlas-2018/bin/woa18.pl and https://www.ncei.noaa.gov/pub/data/paleo/reconstructions/osman2021/). A taxonomically harmonized plankton assemblage dataset (i.e. the combined planktonic foraminifera, dinocyst and coccolithophore data) is available at Zenodo (https://doi.org/10.5281/zenodo.10803875). The R code used to generate the results of this study is available at Zenodo (https://doi.org/10.5281/zenodo.10803875).

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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