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Regional restructuring in planktic foraminifera communities through Pliocene-early Pleistocene climate variability

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Recent studies highlight asymmetrical range shifts within plankton due to spatial variability in climate change, impacting marine ecosystem functioning and biogeochemical cycling. The Pliocene–early Pleistocene interval, characterized by significant climatic fluctuations, provides a framework to study regional responses of marine organisms, such as planktic foraminifera. Using bipartite network analysis of the Triton database, we investigate biogeographic shifts in macroperforate planktic foraminifera ecogroups, tracking taxonomic diversity and distribution. Here we show high turnover between symbiont-bearing warm-water and high-latitude dwellers, isolated to the North Atlantic, and an expansion of cold-water subthermocline taxa across basins, particularly in the South Pacific. Enhanced water column stratification and nutrient export to mesopelagic depths, associated with the intensification of the Northern Hemisphere Glaciation, likely drove shifts in species diversity and ecogroup latitudinal gradients toward modern patterns. This localized community restructuring emphasizes the importance of regional to hemispheric heterogeneity in understanding biodiversity responses to future climate change.

Marine ecosystem services directly impact billions of people. It is essential to understand the response of these ecosystems to ongoing anthropogenic climate changes[1–4]. Given recently documented latitudinal shifts in species ranges[2,3,5], understanding how latitudinal and functional diversity respond to major climatic changes is particularly important. Due to the complexity and short timescale of modern records, exploring pre-historical climate events and the corresponding adaptive response of marine life offers invaluable insights for future ecological trajectories. Here, the deep-sea sediment record, which represents the largest and most complete archive of ancient ecosystem responses to climate change, can help better characterize how biological systems respond to changes in the Earth system.

During the Pliocene–early Pleistocene interval (3.9-1.8 million years ago (Ma)), the planet underwent major climate shifts that shaped both atmospheric and ocean circulation as we know them today e.g., refs. 6–8. These changes began with the rise of the Isthmus of Panama, marking the constriction and closure of the Central American Seaway[9,10] (~5–3.6 Ma). It is important to note that the Central American Seaway closure proceeded in stages: the earlier cessation of deep-water connections, the reduction in surface flow between the Caribbean and Pacific (~5–3 Ma), and the later complete closure that

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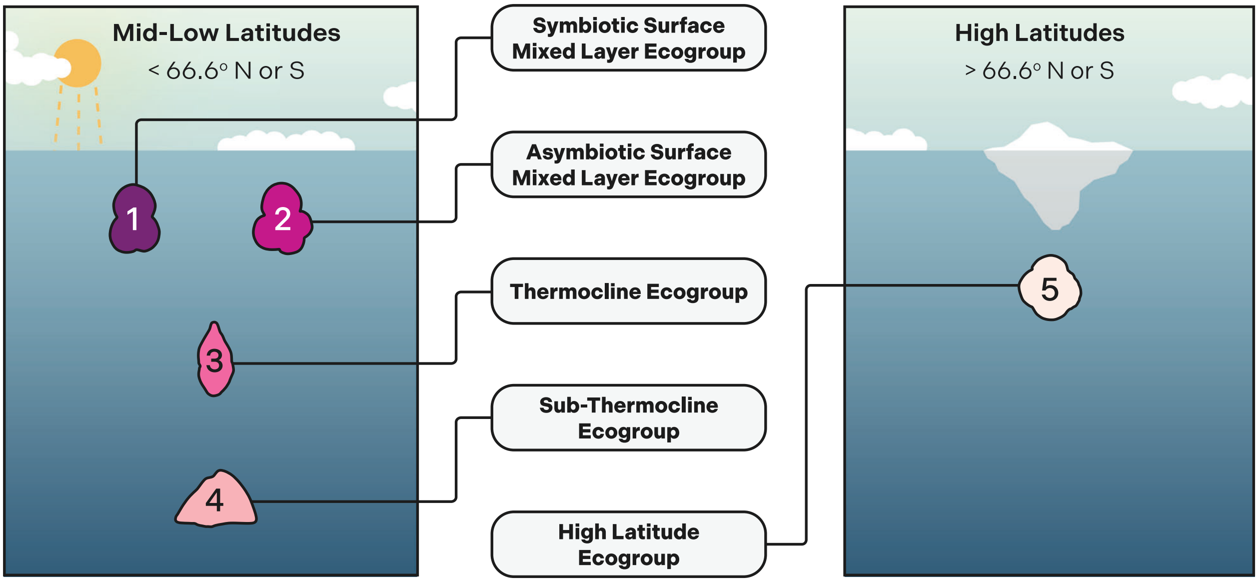


Fig. 1 | A representative diagram of the planktic foraminifera ecogroups used in this study. Ecogroup 1—open ocean surface mixed layer (SML) tropical/subtropical dwellers with algal photosymbionts. Ecogroup 2—open ocean SML tropical/subtropical dwellers without algal photosymbionts. Ecogroup 3—open ocean thermocline dwellers. Ecogroup 4—open ocean sub- thermocline dwellers. Ecogroup 5—high-latitude dwellers. Ecogroup data are from Aze et al.[21]; diagram modified from Woodhouse and Swain et al[3].

prevented faunal migrations between the two ocean basins[7,8] (~ 3 Ma or later). Our study primarily considers the consequences of the earlier closure, which triggered significant reorganization of global ocean circulation, salinity, and heat transport, ultimately contributing to the intensification of the Northern Hemisphere Glaciation[6,7,10]. While the timing of the Central American Seaway closure remains debated[6,8,10,11], we follow the general consensus that significant restriction occurred by ~3.6 Ma[9].

The Pliocene (5.33–2.58 Ma) began with relative cooling, followed by warming during the mid-Piacenzian Warm Period (mPWP) (~3.3–3 Ma). The mPWP is linked to atmospheric CO_2 concentrations similar to the present (380–420 ppm) with global temperatures ~2–3 °C higher than pre-industrial levels[12–14]. This interval provides critical insights into future global climate and biodiversity dynamics, serving as a widely regarded analog to climate change projected for the end of this century[12,13,15,16].

The mPWP was followed by the intensification of the Northern Hemisphere Glaciation (~2.7 Ma), marking the establishment of glacial-interglacial cycles that define the modern climate system[6,17,18]. This transition was marked by global mean cooling of 2–4 °C associated with amplified latitudinal temperature gradients, and increased ocean stratification, seasonality, and regional variability in circulation[19,20]. These oceanographic changes substantially affected pelagic habitats, compressing thermal niches, shifting species distributions, and altering trophic structure[9,20]. The Pliocene–early Pleistocene thus offers a compelling test case to enhance our understanding of marine life responses to anthropogenically-relevant climate change.

Macroperforate planktic foraminifera (single-celled calcareous zooplankton) are a particularly informative fossil group for the study of past climate events because they (1) are an exemplary organism with the most complete species-level fossil record known to science[3,21–25]; (2) are key contributors to the biological carbonate pump[1,26,27] and nutrient cycling[24,28]; (3) generally exhibit thermal niche stability across past climate change events[5,24,29–31]; and (4) are linked to biodiversity of important pelagic groups, including sharks, krill, and squid, amongst others[3,32,33]. Additionally, their distinctive carbon and oxygen stable isotope signatures offer invaluable insights into their vertical position within the water column[21], allowing for the assignment of extant and extinct species into discrete ecological niche groups (ecogroups) (Fig. 1; Supplementary Table 1-2). In the context of a warming ocean, the thermal niche stability of planktic foraminifera is a significant concern, due to their tendency to track rather than adapt to temperature shifts, likely affecting their future distribution and the trophic dynamics of associated organisms[1,4,5,34]. Asymmetrical range shifts in modern plankton communities, partially driven by the spatial heterogeneity of climate change, significantly impact the structure and functioning of pelagic ecosystems[34–36]. Understanding the drivers and consequences of these shifts requires high- resolution temporal and spatial data that can link past biodiversity patterns to environmental changes.

Although comprehensive studies of planktic foraminiferal diversity over various temporal scales, ranging from thousands[34,37,38] to millions[3,39] of years, exist; to date, few have investigated regionally resolved patterns across intermediate timescales using hundreds of sites. The recently collated Triton dataset, which provides an extensive record of global fossil occurrences of planktic foraminifera[22], enables high-resolution analyses of species diversity and functional dynamics of planktic foraminifera. This dataset offers new opportunities to investigate shifts in vertical ocean temperature structure and the corresponding responses of plankton populations to paleoclimate change at regional scales[3,22], with relevance to ongoing and future climate crises.

Here, we use the Triton database to assess spatial and ecological patterns of macroperforate planktic foraminifera across the Pliocene–early Pleistocene interval (3.9 Ma–1.8 Ma), focusing on biogeographic shifts in ecological groups and standing species diversity. Our basin-scale analyses cover the Atlantic ($n = 21{,}547$ species occurrences, 127 sediment cores), Pacific ($n = 18{,}834$ species occurrences, 156 sediment cores), and Indian ($n = 10{,}459$ species occurrences, 87 sediment cores) oceans[22], with temporal resolution of 150 kyr (thousand years). By integrating basin-scale analyses with ecological niche metrics such as the Ecogroup Specialization Index (ESI), we reveal distinct patterns of ecological restructuring and hemispheric heterogeneity that are not evident in global averages lacking spatial context e.g., ref. 3. We show that the Pliocene–early Pleistocene period was a time of significant reorganization of planktic foraminiferal communities, characterized by variability in the response of ecogroups and species diversity across different ocean basins. Specifically, we find high turnover between symbiont-bearing tropical taxa and high- latitude dwellers isolated to the North Atlantic, alongside a trans-basin expansion of cold-water subthermocline taxa, most prominently in the South Pacific. Enhanced water column stratification and mesopelagic nutrient export associated with the intensification of Northern Hemisphere Glaciation possibly drove these shifts. This approach enhances our understanding of how regional and temporal variations of environmental drivers shaped marine biodiversity during this pivotal interval.

Results

Bipartite network analysis and data validation

Network studies, particularly bipartite network analyses, have been increasingly applied in paleoecology to explore the complex relationships between species, environments, and ecological interactions across deep time[3,39]. Bipartite networks have been used to reconstruct trophic interactions[40,41], examine latitudinal biodiversity patterns, and assess species-environment dependencies during key climatic and geological events[3,39]. These methods provide a framework for understanding how species co-occurrences and ecological roles vary spatially and temporally, offering insights into species turnover, extinction events, and ecosystem restructuring in response to past environmental changes[3,39,42].

Here we implemented bipartite network analyses following the methods outlined in Woodhouse and Swain et al.[3], which consist of two classes of nodes: ecogroups as one class and 5° palaeolatitudinal bands as the other. Links in these networks represent the biogeographical co-occurrences between ecogroups and palaeolatitudinal bands, providing a holistic and innovative approach to capture their interconnected nature. In the bipartite network analysis, the width of the links between an ecogroup and a palaeolatitudinal band denotes the number of occurrences of that ecogroup at a given palaeolatitudinal band within that temporal bin (see Methods).

To address potential sampling biases between hemispheres and basins, we performed resampling of ecogroup distribution data without replacement ($n = 1000$) for each 150 kyr time bin, matching the smallest number of cores in any 150 kyr bin (Supplementary Fig. 9). This analysis revealed that both raw and subsampled datasets exhibit identical distributions, indicating that observed patterns are not influenced by sampling differences. Additionally, sampling coverage metrics and Pielou's Evenness confirmed high data completeness and consistent representation of ecogroup distributions across regions (Supplementary Figs. 13–17).

After verifying robust sampling coverage and evenness, we calculated the Ecogroup Specialization Index to investigate biogeographic patterns across paleolatitudes at a 150 kyr resolution for the Atlantic, Pacific, and Indian oceans during the Pliocene—early Pleistocene (Fig. 2). The ESI quantifies the degree of evenness in the distribution of ecogroups within a paleolatitudinal band relative to other bands in each temporal bin. Lower ESI values (bluer colors in Fig. 2b, d, f) indicate higher evenness, where all functional groups are equally represented within a paleolatitudinal band. In contrast, higher ESI values (more yellow colors in Fig. 2b, d, f) correspond to dominance by a single group (for further methodological details, see the Methods section). To further validate our results on species specialization, we ran null models to evaluate deviations from random expectations of occurrences while accounting for spatiotemporal constraints (Supplementary Figs. 10–12; see Methods section for details).

We examined five ecogroups, previously classified by Aze et al.[21] based on their stable isotopic geochemical fingerprint and biogeography: ecogroup 1, mixed layer tropical/subtropical species with symbionts; ecogroup 2, mixed layer tropical/subtropical species without symbionts; ecogroup 3, thermocline species; ecogroup 4, subthermocline species, and ecogroup 5, high- latitude species (Fig. 1). We constructed a table of extant species of planktic foraminifera and compared their ecogroup classifications from Aze et al.'s[21] evaluation to modern plankton tow and sediment trap studies, finding a strong correlation between the two (see Supplementary Table 1).

The benefit of assessing community structure through the lens of functional groups, such as ecogroups, is their consistency over geological time, irrespective of the contemporaneous evolution and extinction of individual species within said groups[3]. Ecogroup data allows quantitative investigations of ecological niche space occupation in the past and its response to global climate change.

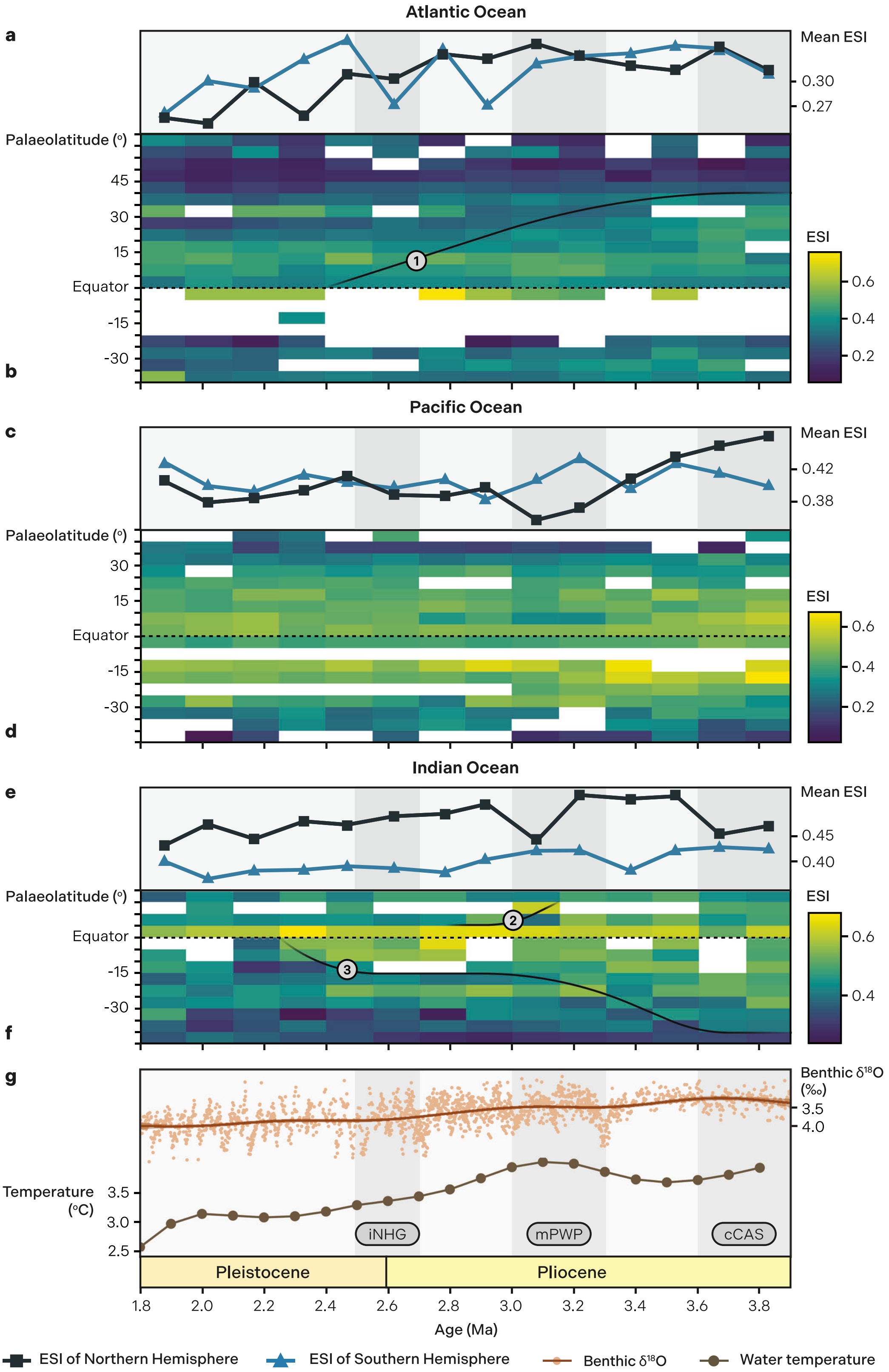
Woodhouse and Swain et al.[3] analyzed the global record of planktic foraminiferal ESI, demonstrating that zones with low ESI had migrated equatorward over the past ~8 Myr. Their findings focused on a global compilation; however, recent studies of zooplankton dynamics suggest a high degree of regional heterogeneity to global change[31]. It is, therefore, important to examine metrics such as ESI and species diversity on a basin-scale to comprehensively understand how different ocean basins respond to climate shifts and how regional changes contribute to the global average.

Spatial patterns in Ecogroup Specialization Index

In our study, the lowest ESI zones, indicative of the highest ecogroup evenness, are predominantly located in mid-latitude regions compared to lower latitudes across all basins (Fig. 2b, d, f). These mid-latitude zones align with areas of higher species richness[3,43] and species turnover areas[31]. This distribution pattern potentially results from steeper vertical temperature gradients at mid-latitudes, which foster stratification of vertically stacked niches, accommodating a large variety of equally represented ecogroups[3,43]. Following the mPWP, a shift in decreased ESI from mid-latitudes to lower latitudes is observed in the North Atlantic and southern Indian oceans (Fig. 2b, f). These collective shifts manifested an equatorward movement of global ecogroup evenness (or equitability) zones, as noted by Woodhouse & Swain et al.[3]. It is important to note that our study excludes high-latitude data due to a lack of continuous temporal and spatial coverage. A study of the last 20,000 years by Jonkers et al.[31], a period with climate perturbations much stronger than those recorded during our study interval, identified key biogeographic changes at mid-latitudes, aligning with the latitudinal limits of our analysis.

Hemispheric variability in ecogroup distributions

To assess the hemispheric-scale variability in ESI and identify the specific ecogroups contributing to these fluctuations, we calculated the average ESI (Fig. 2a, c, e) and the proportional distribution of each ecogroup for each hemisphere in each ocean basin over time (Fig. 3; Supplementary Figs. 2–7). The most prominent decrease in ESI occurred in the North Atlantic between 3.1 and 1.8 Ma, driven by increased relative occurrences of high-latitude (ecogroup 5) and subthermocline (ecogroup 4) dwellers, coupled with decreased relative occurrences of symbiotic surface mixed layer dwellers (ecogroup 1) (Figs. 2a, 3; Supplementary Figs. 2–3,6,7). Our linear model highlights a negative correlation restricted to the North Atlantic, specifically between the warm-water taxa of ecogroup 1 and the high-latitude, cool-water taxa of ecogroup 5. The negative correlation emerged concurrently with the onset of the intensification of the Northern Hemisphere Glaciation at ~2.7 Ma, and ecogroup 5 played a significant role in driving the observed ecological changes during the Pliocene—early Pleistocene interval (Supplementary Fig. 8). The population of ecogroup 5 in our study is represented by only two species—*Neogloboquadrina pachyderma* and *Turborotalita quinqueloba*—in contrast to other ecogroups (See supplementary Table 1). Despite its lower diversity, ecogroup 5 plays a significant role in driving changes observed during the Pliocene—early Pleistocene interval. It is important to note that *Neogloboquadrina atlantica*, although known to be common in the North Atlantic during the study interval, was excluded



from our study due to a low number of records in the Triton dataset, likely a result of historical misidentification and synonymization with other taxa. While its absence does not affect the broader interpretations presented here it highlights the importance of continued taxonomic refinement in future iterations of the database.

The ESI decline in the South Atlantic was less pronounced and began at ~3.5 Ma (Fig. 2a, b). In the North Pacific, a steeper ecogroup evenness gradient was observed between 3.9 and 3.2 Ma, followed by an increase in ESI after the mPWP (Fig. 2c, d). This variation in ecogroup evenness is primarily driven by a decrease in the relative abundance of thermocline dwellers (ecogroup 3) and an increase in high-latitude dwellers (ecogroup 5) during these periods (Fig. 3; Supplementary Figs. 2, 5b, 7b). Conversely, ESI remained relatively flat in the Southern Hemisphere of the Pacific, suggesting stable vertical

Fig. 2 | Environmental proxies for the Pliocene–early Pleistocene Climate and Ecogroup Specialization Index. a–e The Ecogroup Specialization Index (ESI) is calculated for each hemisphere. The black line (squares) represents the Northern Hemisphere (NH), and the blue line (triangles) represents the Southern Hemisphere (SH). A bipartite network quantifies the Latitudinal Evenness (or Equitability) Gradient or ESI among ecological groups in the Atlantic Ocean (**b**) Pacific Ocean (**d**) and Indian Ocean (**f**). The ESI quantifies how even the distribution of ecogroups is within a paleolatitudinal band relative to others in each temporal bin. Lower ESI values (denoted by blue colors) indicate higher evenness, where all functional groups are equally represented within a paleolatitudinal band. In contrast, higher ESI values (denoted by yellow colors) correspond to dominance by a single group. The white areas in the figure represent data gaps or bins that did not meet the data completeness criteria and were consequently excluded from the analysis. (**g**) Benthic δ^{18}O from Westerhold[72]. Temperature estimates are based on Mg/Ca values in Pacific cores from Cramer[73]. The oxygen isotope data have been smoothed using a generalized additive model (brown line), which represents the predicted mean. The gray shading indicates 95% confidence interval of the fitted mean. Gray vertical panels indicate important Pliocene–early Pleistocene events; cCAS closure of the Central American Seaway, mPWP the mid-Pliocene Warm Period, iNHG the intensification of the Northern Hemisphere Glaciation. The North Atlantic (**a**, **b**) underwent the most significant change, marked by the migration of zones with low ecogroup specialization (in blue) towards the equator (black line **1**; (**b**) and the mean ESI decrease in the Northern Hemisphere (**a**) immediately following the mPWP. Black lines (**2**, **3**) in the Indian Ocean (**f**) capture localized variations in specialization gradients, reflecting ecological restructuring during the studied interval. These patterns underscore regional heterogeneity in response to climatic and environmental changes. Source data are available at https://zenodo.org/records/15344269.

temperature gradient conditions during this interval (Fig. 2c). As the climate began to cool again following the mPWP (Fig. 2g), there was an increase in the proportion of subthermocline dwellers (ecogroup 4) across all basins, with the highest rate of expansion in the Southern Hemisphere (Fig. 3; Supplementary Fig. 2, 6).

Temporal shifts in species and ecogroup diversity

To gain insights into standing diversity and functional dynamics across the Pliocene–early Pleistocene, we analyzed the corrected sample-in-bin metric[44], using shareholder quorum subsampling (SQS), of both species and ecogroup diversity (Fig. 4; see Methods). The modern latitudinal diversity gradient of planktic foraminifera was established ~15 Ma, where diversity increases towards lower latitudes with a slight equatorial depression[3,28,45,46]. Studies of planktic foraminiferal global biodiversity document a species diversity peak in the Pliocene[43] followed by a decline towards modern levels[3,37]. Our data reveal that this trend occurred asynchronously, characterized by hemispheric heterogeneity (Fig. 4). The decline in species diversity initiated across all studied ocean basins in the Southern Hemisphere coincided with the mPWP. This was subsequently followed by a decline in planktic foraminiferal diversity across both hemispheres coinciding with the onset of the intensification of the Northern Hemisphere Glaciation (Fig. 4a).

The decoupling of ecogroup and species diversity across the Pliocene–early Pleistocene is observed in all ocean basins (Fig. 4). The most significant changes in ecogroup diversity occurred in both the North Atlantic and North Pacific, although these shifts occurred during different time frames (Fig. 4b). In the North Atlantic, ecogroup diversity began increasing immediately after the mPWP. In the North Pacific, ecogroup diversity increased between 3.6 and 3.0 Ma (Fig. 4b). In the Indian Ocean, ecogroup diversity remained relatively stable in the Northern Hemisphere, while the Southern Hemisphere displayed a gradual increase between the closure of the Central American Seaway and the onset of the mPWP. Overall, these shifts in ecogroup diversity appear to occur over a broad interval spanning the closure of the Central American Seaway, the mPWP, and the intensification of the Northern Hemisphere Glaciation, rather than being tightly constrained to a specific event. We note, however, that the confidence intervals for ecogroup diversity often overlap, especially in the Atlantic and Pacific oceans (Supplementary Fig. 19), which limits the statistical support for some of these observed differences across time and space.

Discussion

During the Pliocene–early Pleistocene, following the closure of the Central American Seaway (~3.6 Ma), planktic foraminiferal communities underwent substantial and systematic rearrangement, marked by hemispheric and basinal heterogeneity (Figs. 2–4). Minimal variations in ecological and biodiversity dynamics occurred between 3.9 and 3.5 Ma. This relative stability could be attributed to either the closure of the Central American Seaway, which exerted limited additional influence on planktic foraminiferal communities, or more likely that the critical changes had already taken place earlier—prior to the "final" closure recognized in macrobenthic invertebrates from Central America ref. 8.

In contrast, the mid-Piacenzian Warm Period marked notable shifts in ecogroup dynamics, particularly within the North Pacific. During this interval, the proportional abundances of high-latitude (cool-water; ecogroup 5) and subthermocline (deep-water; ecogroup 4) ecogroups increased, while thermocline (ecogroup 3) and symbiotic warm-water dweller (ecogroup 1) populations decreased (Fig. 3). These shifts may reflect thermocline shoaling, a phenomenon previously documented in the North Pacific[19,47]. Similar results were reported from the Eastern Equatorial Pacific[48], with an increased abundance of cool and deep-water taxa following the mPWP. Paradoxically, the dominance of high-latitude, cool-water taxa (ecogroup 5) took place during the ongoing mPWP. This pattern may be explained by a warming of the Kuroshio Current Extension in the northern Pacific, which consequently developed strong temperature and salinity gradients at mid-latitudes[49]. In combination with cool subpolar waters brought south by the Oyashio Current, this could have created a prominent ecotone for several communities[49,50].

The mid-Pliocene interval also likely overlapped with variations in overturning states, as recent modeling evidence supports the presence of an active Pacific Meridional Overturning Circulation during the mPWP, which may have influenced thermocline shoaling and stratification in the North Pacific[19]. Together with surface currents, these changes in overturning circulation underscore the importance of regional oceanographic variability in shaping ecological patterns. Simultaneously, the mid-Pliocene interval overlapped with the progressive closure of the Central American Seaway, the onset of the intensification of the Northern Hemisphere Glaciation, and a stronger Atlantic Meridional Overturning Circulation (AMOC)[8]. Intensification of AMOC significantly influenced the redistribution of heat from the poles to the equator, facilitating the gradual cooling and shoaling of the thermocline[51]. Furthermore, despite these climatic shifts, species diversity remained largely unaffected in both the North Atlantic and North Pacific oceans (Fig. 4a), indicating resilience in these regions to the warming event[9] despite the changes in latitudinal and vertical temperature gradients. In contrast, the North Indian Ocean experienced a notable decline in species diversity beginning around 3.8 Ma, followed by a rebound during the mPWP (Fig. 4a). This decline likely reflects significant regional environmental changes driven by shifts in ocean circulation and monsoon dynamics. During this time, the shoaling of the Indonesian Throughflow[52] reduced the transport of warm, nutrient-poor waters into the Indian Ocean, potentially altering thermocline structure and surface stratification.

The largest transformation of macroperforate planktic foraminifera assemblages was potentially linked to the expansion of ice sheets in the Northern Hemisphere during the late Pliocene, with the North Atlantic exhibiting the highest rates of change[29] (Figs. 2–5; Supplementary Figs. 3a, 7a). This phenomenon could be due to the

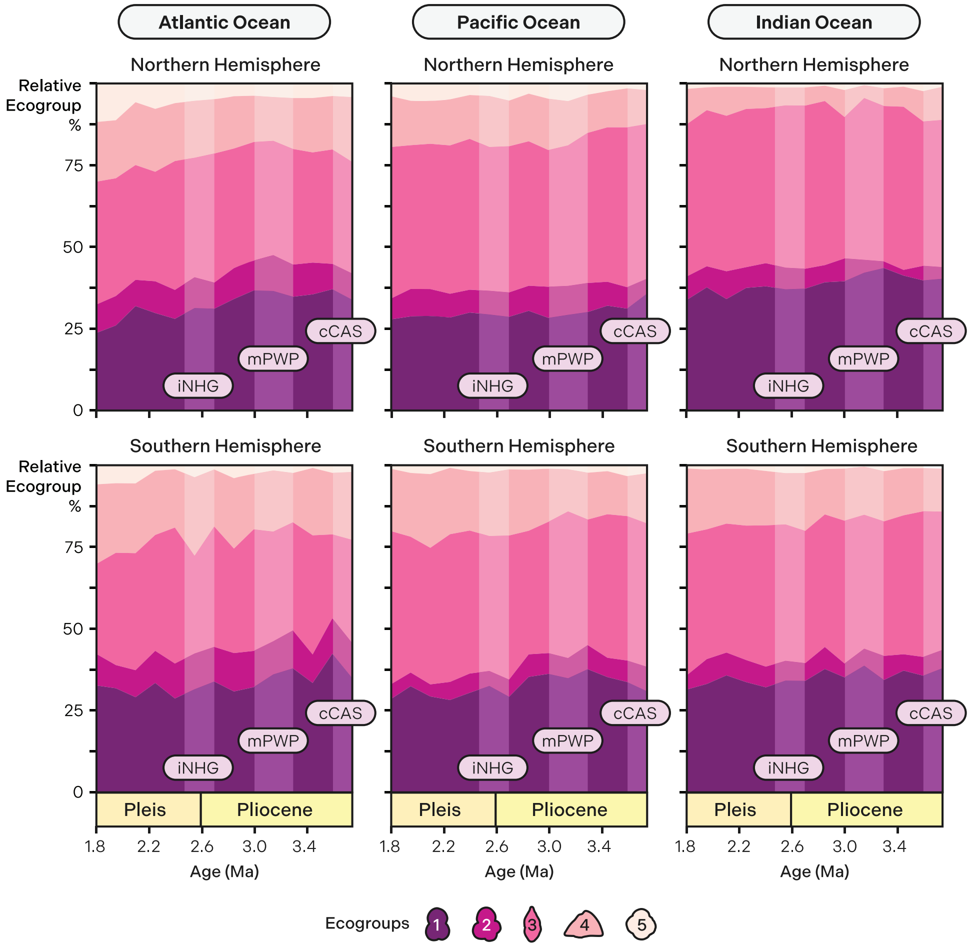


Fig. 3 | Relative percentage of each ecogroup in three ocean basins across the Pliocene–early Pleistocene. The highest rate of change was observed in the North Atlantic, marked by an increase in ecogroup 5 and a decrease in ecogroup 1, coinciding with the onset of the intensification of the Northern Hemisphere Glaciation. cCAS closure of the Central American Seaway; mPWP the mid-Pliocene Warm Period, iNHG the intensification of the Northern Hemisphere Glaciation, Pleis Pleistocene. Ecogroup 1—open ocean surface mixed layer (SML) tropical/subtropical dwellers with algal photosymbionts. Ecogroup 2—open ocean SML tropical/subtropical dwellers without algal photosymbionts. Ecogroup 3—open ocean thermocline dwellers. Ecogroup 4—open ocean sub-thermocline dwellers. Ecogroup 5—high-latitude dwellers. Source data are available at https://zenodo.org/records/15344269.

region's proximity to major Northern Hemisphere ice sheet expansion and the intensified AMOC[53]. Ocean cooling during this period could have enhanced water column stratification, allowing for a more evenly distributed vertical arrangement of ecogroups across latitudes shifting low ESI zones equatorward[3,43] across both the North Atlantic and Indian oceans (Fig. 2b, f). Oceanic cooling also might have contributed to a decrease in the rate of remineralization of sinking organic matter[28]. As a result, more organic material would have reached the mesopelagic zone[28] providing an increased food supply to deep- water dwellers; elevated nutrient availability would have enabled sub-thermocline populations to grow[28].

Overall, the interplay between regional overturning circulation (e.g., AMOC and Pacific Meridional Overturning Circulation) and cooling during the intensification of the Northern Hemisphere Glaciation could catalyze a reconfiguration of latitudinal diversity and evenness gradients towards modern levels[3]. These compounded Earth system changes would have facilitated ecological niche rearrangement of high-latitude (ecogroup 5) and symbiotic warm-water (ecogroup 1) dwellers in the North Atlantic, alongside biogeographic range expansion of subthermocline dwellers (ecogroup 4) across all basins, most notable in the Southern Hemisphere (Fig. 3; Supplementary Figs. 3, 6, 7). Despite the boost in ecogroup diversity, observed taxonomic diversity declines are likely a consequence of extinction and extirpation rates surpassing origination rates[9,42,43,54] (Fig. 4). Nevertheless, loss of morphological species may have been offset by an increase in genetic types as suggested by Woodhouse et al.[48]. These results provide important constraints on marine organism responses to substantial environmental change. Our study highlights the importance of capturing the spatial heterogeneity of these responses by conducting comparative studies at regional scales (as opposed to local or global averages), as climate shifts from its pre-industrial state.

Insights into the future of warming oceans

Our study offers valuable perspectives on the potential future trajectories of biodiversity and functional dynamics in calcareous plankton and other critical marine species, whose biogeographic patterns closely align with those of the planktic foraminifera[1,3,32,33]. These findings suggest that ecogroup 2 and ecogroup 3 taxa (asymbiotic mixed layer and thermocline dwellers, respectively) may be the least impacted by imminent ocean warming (Fig. 5). Conversely, symbiont-bearing species living in the mixed layer (ecogroup 1) may experience forced poleward migration[3,55]. Similarly, species at higher trophic levels are expected to migrate towards the poles, mirroring the movements of calcareous zooplankton, since both are influenced by comparable principal ecological dynamics[1,34,56]. Though species diversity of planktic foraminifera might remain stable, functional diversity is at risk of significant decline due to a reduction in water column stratification

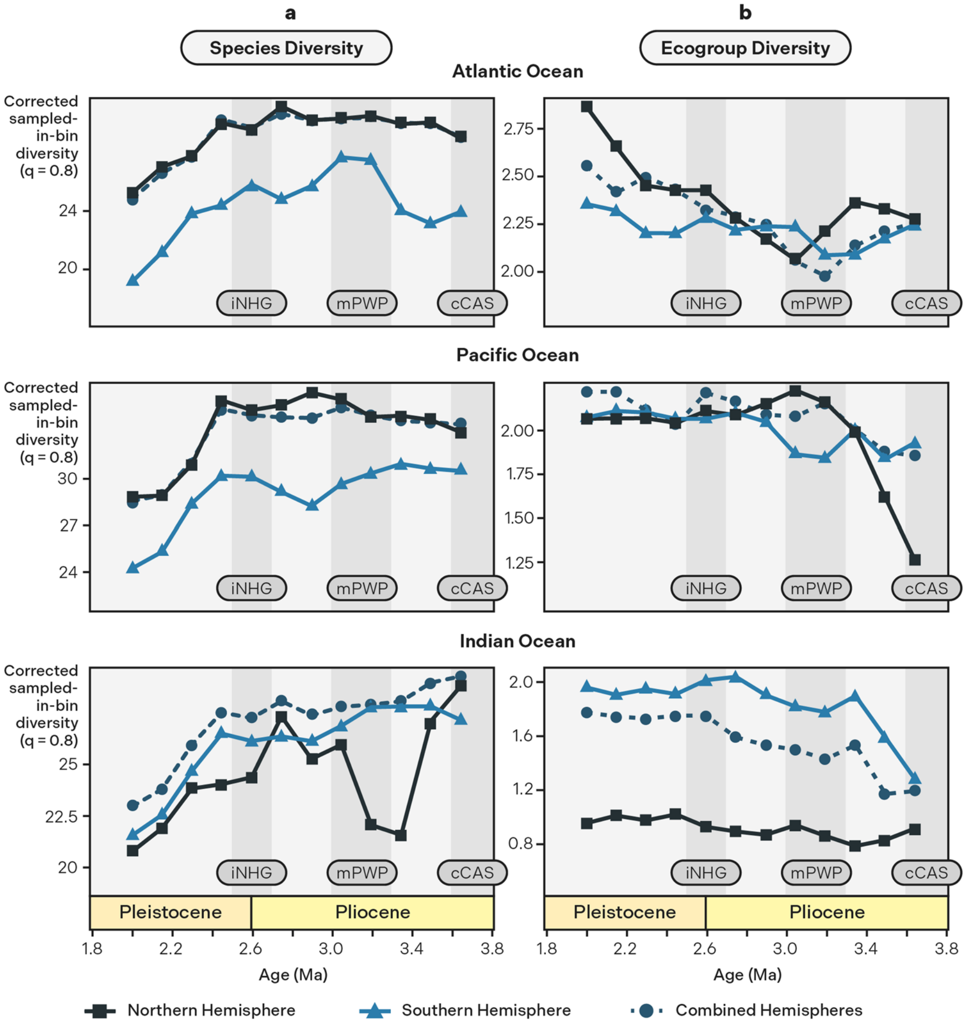


Fig. 4 | Corrected sampled-in-bin diversity across the Pliocene–early Pleistocene in the Atlantic, Pacific, and Indian Oceans. Values are based on sample-standardized data using shareholder quorum subsampling method with corrected sampled-in-bin diversity by (**a**) species and (**b**) ecogroup. Across the Pliocene–early Pleistocene, there is a decoupling between ecogroup and species diversity of planktic foraminifera, with species diversity decline coinciding with the intensification of the Northern Hemisphere Glaciation. cCAS closure of the Central American Seaway, mPWP the mid-Pliocene Warm Period, iNHG the intensification of the Northern Hemisphere Glaciation. Source data are available at https://zenodo.org/records/15344269.

that may result from rising temperatures. Warming oceans are expected to hinder the transport of particulate organic carbon and oxygen to the mesopelagic zone[28], leading to a contraction of sub-thermocline ecological niches[57]. The invasion of warm water taxa poleward due to the expansion of their biogeographic ranges will likely cause an increase in turnover rates of high latitude taxa, with unknown consequences for polar populations[1,58].

The North Atlantic is anticipated to continue being a center of significant environmental changes, largely owing to the sensitivity of AMOC to climate-driven shifts[31,59] and the strong impact of sea surface temperature on planktic species distribution in the region[1,29,34,38]. Coastal upwelling areas, like the Peruvian upwelling in the Pacific, are predicted to remain zooplankton diversity hotspots[1], with enhanced food availability mitigating temperature-induced declines[60]. Our results suggest that the Pacific Ocean and Indian Ocean basins will experience a lower rate of change compared to the North Atlantic[1,4]; that said, existing records in the Indian Ocean and parts of the Pacific are fewer, making it challenging to predict their marine zooplankton dynamics[1,4,18]. Ultimately, the spatial heterogeneity of climate change will persist as a key factor causing the discrete and localized restructuring of planktic foraminifera, as demonstrated from the fossil record responses analyzed here. It is imperative to further enrich our knowledge of planktic foraminiferal evolution and ecosystem functioning in the coming years.

Methods

Data

We quantified the spatiotemporal shifts of macroperforate planktic foraminifera using a total of 50,840 species-by-locality-by-age records from the Triton dataset; specifically with 21,547 unique occurrences from the Atlantic (number of cores = 127), 18,834 unique occurrences from the Pacific (number of cores = 156), and 10,459 unique occurrences from the Indian oceans (number of cores = 87) (Supplementary Fig. 1). Planktic foraminifera with microperforate and medioperforate wall textures were excluded from the analysis since they are currently characterized by a less refined phylogeny compared to macroperforate forms[21,61]. In addition, the relative lack of ecogroup assignments among microperforate species, only 43 out of 81 in the latest phylogeny, would significantly limit the completeness and comparability of the dataset. For our analysis, speciation and extinction data for all macroperforate planktic foraminiferal species were determined based on the frameworks provided by Aze et al.[21] and Fenton & Woodhouse et al.[22]. We excluded any species occurrences falling outside their established

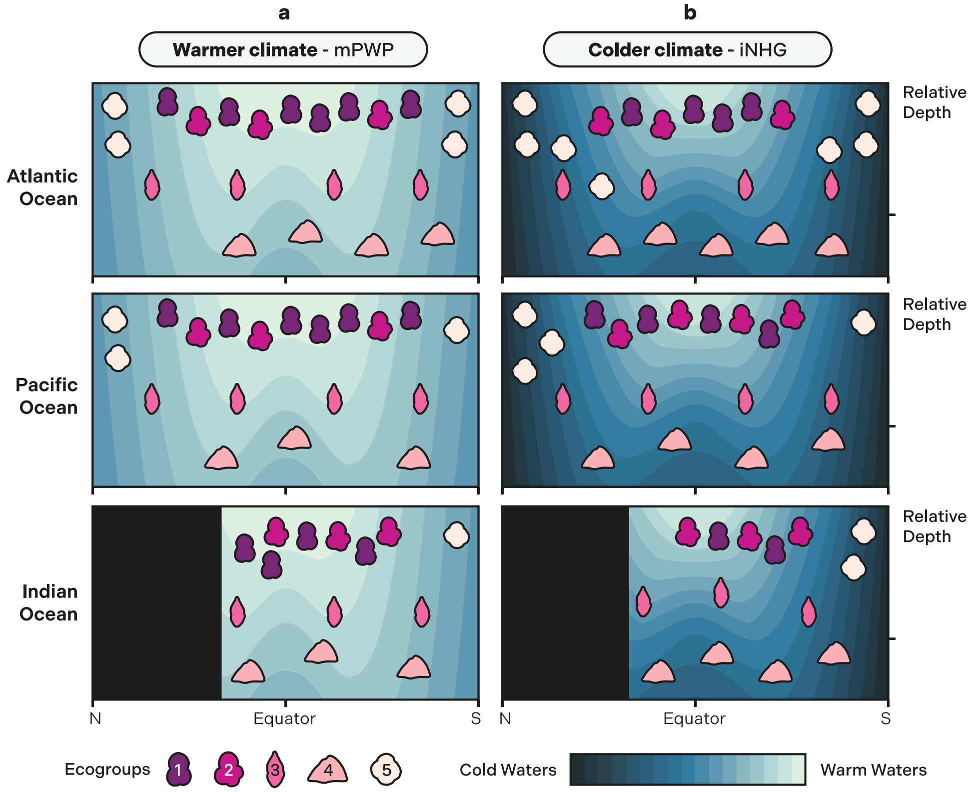


Fig. 5 | Planktic foraminiferal ecogroup distributions during warm and cold climate states. Conceptual representation of ecogroup distributions during warmer (mPWP the mid- Pliocene Warm Period) (**a**) and colder (iNHG the intensification of the Northern Hemisphere Glaciation) (**b**) climate regimes across ocean basins. Warmer climates (mPWP) (**a**) are characterized by a greater equatorial dominance of symbiotic mixed-layer species (ecogroup 1), while colder climates (iNHG) (**b**) exhibit increased latitudinal stratification and an expansion of high-latitude species (ecogroup 5) in the Atlantic and North Pacific. In the Indian Ocean, the transition from warmer to colder climates is primarily marked by a decrease in ecogroup 1 and an increase in ecogroup 4. Ecogroup 2 and ecogroup 3 taxa (asymbiotic mixed-layer and thermocline dwellers, respectively) are the least impacted by climate variations. Ecogroup 4 increased its abundance across Southern Hemisphere basins during the iNHG.

stratigraphic ranges to minimize inaccuracies in the occurrence data likely resulting from misidentification or stratigraphic reworking. We included a total of 74 species of planktic foraminifera, comprising 36 extant species and 38 extinct species (see Supplementary Table 1). Raw counts of each species within each ecogroup, binned in 150 kyr intervals, are provided in Supplementary Data 1. The studied interval covered the Pliocene–early Pleistocene, spanning from 3.9 to 1.8 Ma, and utilized foraminiferal data categorized into 150 kyr time bins, which were further divided into paleolatitudinal bands of 5°. In our study, the Atlantic Ocean dataset included 226 combined time-latitude bins, the Pacific Ocean included 207 bins, and the Indian Ocean included 162 bins.

To investigate whether species ecology played a role in their biogeographic network interactions across the Pliocene–early Pleistocene, we also assigned species to the five specified ecogroups from Aze et al.[21]. Ecogroups are defined as following: ecogroup 1, mixed layer tropical/subtropical species with symbionts; ecogroup 2, mixed layer tropical/subtropical species without symbionts; ecogroup 3, thermocline species; ecogroup 4, sub-thermocline species, and ecogroup 5, high-latitude species (Fig. 1; Supplementary Table 1, 2). Ecogroups are determined by examining the biogeographic distributions, phylogenetic relationships, and the stable oxygen ($\delta^{18}O$) and carbon ($\delta^{13}C$) isotopic signature of planktic foraminiferal species skeletons. These analyses allow us to assess the extent of bathymetric and ecological differentiation among both extant and extinct species enabling us to deduce species-specific ecological niches, influenced by varying physicochemical and biological processes, as well as depth-related variations within the water column[21,48,62].

Calculating network-associated ecological metrics

In this study, we used the modified Triton dataset[22], partitioning planktic foraminifera into 150 kyr time bins and 5° paleolatitude bands. We constructed bipartite networks using these bins where paleolatitude represented one node class and ecogroup the other node class. Bipartite networks are used to analyze interactions between two distinct sets of nodes and can provide insights into the ecological structure and relationships within datasets such as Triton. The links between these nodes represent the presence of a certain ecogroup within a specific paleolatitudinal band, where the width of these connections indicates the frequency of each ecogroup's occurrence in the respective paleolatitudinal band[6,58]. To assess dataset completeness, we examined the sampling coverage (frequency of each unique ecogroup within a paleolatitudinal band during each time interval) using the *iNEXT* v3.0.1 R[63] package, which is based on Good's U estimator[64,65]. Our analysis showed that all samples achieved sufficient and consistent coverage levels for our interpretations (See Supplementary Figs. 13, 14, 17).

The *bipartite* package[66] v2.20 in R v4.3.2 calculated network-associated ecological metrics for each paleolatitudinal band node: (1) number of ecogroups at that paleolatitudinal band, and (2) the Ecogroup Specialization Index (ESI). The ESI calculates the coefficient of variation in the number of occurrences of ecogroups within a particular paleolatitudinal band, with its values normalized to a range between 0 and 1. Here, a value of 0 signifies low specialization, indicating generalized functional communities with an even distribution of ecogroups, whereas a value of 1 suggests high specialization, indicative of specialized functional communities dominated by one ecogroup.

This index is based on the Species Specificity Index concept introduced by Julliard[67] and Poisot[68] (see cited papers for detailed explanation), tailored to quantify the uniformity or disparity in ecogroup distribution across a paleolatitudinal band for each time interval. Thus, a band characterized by an identical occurrence count for all ecogroups would exhibit an ESI of 0 (dark blue in Fig. 2), whereas a band dominated by a single ecogroup would display an ESI approaching 1 (yellow in Fig. 2). The ESI is weighted by the relative occurrence counts of different 397 ecogroups within a paleolatitudinal band. To address potential biases, such as the underrepresentation of depauperate ecogroups (e.g., the polar group), we calculated ESI using relative frequencies rather than raw counts, ensuring proportional contributions. Additionally, we used null model analyses to interpret the ESI robustly and identify statistically significant patterns of specialization (See Supplementary Figs. 10–12 for a summary of these patterns across ecogroups).

To understand species specialization within a biogeographical framework and determine how observed patterns deviate from random expectations, we utilized the *econullnetr* v0.2.1 R package[69]. These null models simulate the distribution of various ecogroups across each latitudinal band while accounting for (1) the number of occurrences across all ecogroups within specific latitudinal bands, and (2) the temporal occurrences within ecogroups across all latitudes. We generated 500 sampling distributions by iterating the null model and calculated 95% confidence intervals for occurrence frequencies of each ecogroup within each latitudinal and time bin. If the empirical occurrence frequencies fall outside these confidence intervals, occurrence values are either significantly greater or less than expected under a random distribution. This method provides a statistical framework for detecting deviations and interpreting specialization trends calculated from the observed occurrence values (see Supplementary Figs. 10–12 for a summary of these patterns across ecogroups). As most ecogroups do not show significantly different distributions from the null expectations, the results suggest that shifts in community composition over time are primarily driven by temporal or environmental changes rather than fixed biogeographic or regional constraints.

Species and ecogroup diversity

To explore the standing diversity of species and functional dynamics of planktic foraminiferal ecogroups across the Pliocene–early Pleistocene Period, we conducted the analysis based on the corrected sample-in-bin metric, utilizing the shareholder quorum subsampling (SQS). The corrected sampled-in-bin metric is used to account for sampling biases when estimating the presence of taxa within a specific time bin[44]. It adjusts the observed data to better reflect true ecological or evolutionary signals by correcting for variations in sampling effort across different intervals. This approach is particularly useful in paleontological and ecological studies to avoid over- or under-representing taxa due to uneven sampling[70]. To mitigate the effects of uneven sampling intensity across different times and locations for species and ecogroups, the SQS quorum level was set at 0.8 and we ran 1000 iterations in 150 kyr time bins using the *divDyn* v0.8.2 R package[71].

The SQS method is designed to normalize raw species richness to a consistent share of the total frequency distribution. Its key strength lies in its enhanced ability to include rare taxa in the analysis, providing a more comprehensive and accurate representation of biodiversity[70]. The standing diversity is characterized by the corrected sample-in-bin metric, which is an assessment of the richness of both species and ecogroups over time, thereby providing a more refined understanding of ecological and evolutionary trends during the studied interval.

Ecogroup trends and variability

To elucidate temporal trends in ecogroup distribution and identify specific ecogroups contributing to the variability of the ESI in the Atlantic, Pacific, and Indian Ocean basins, we calculated the relative abundance of each ecogroup within 15 kyr time bins. Initially, we performed resampling of ecogroup distribution data without replacement 1000 times for each 150 kyr time bin, matching the smallest number of cores observed in any 150 kyr bin. Subsequent analysis of both the original dataset and the subsampled datasets revealed congruent distributions, affirming that patterns and trends in the ecogroup distribution and ESI variability are robust and not artifacts of sampling (Supplementary Fig. 9).

To quantify the rates of change in the relative abundance of each ecogroup across hemispheres and basins, we calculated the slopes of these fitted linear models for ecogroup relative abundance over time. A positive slope indicates an increase in the number of ecogroup dwellers from 3.9 to 1.8 Ma, while a negative slope indicates a decrease. Time series showing a decreasing proportion of ecogroup occurrences over time are characterized by a negative slope, and vice versa (Supplementary Figs. 3–7).

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

Source data for all figures are available at Zenodo: https://doi.org/10.5281/zenodo.15344269.

Code availability

Code is available at https://github.com/ekatlarina/forams-ecogroups and https://doi.org/10.5281/zenodo.15344269.

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Author contributions

E.L. developed the study concept, generated the data, and conducted the analyses. E.L., A.W., A.S., C.M.L., R.C.M., and C.E.M. contributed to the interpretation of data. E.L. conceived and plotted the figures. E.L. wrote the first draft and A.W., A.S., C.M.L., R.C.M., and C.E.M. contributed to the final draft of the paper.

Competing interests

The authors declare no competing interests.

Additional information

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