# Long-term response of marine plankton to climate change in the North Atlantic Ocean during the past 24,000 years

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# Affirmation in lieu of an Oath

*according to § 5 (5) of the Doctoral Degree Rules and Regulations of 18 June, 2018*

I, Tonke Strack, [redacted], Student ID: [redacted]

With my signature I affirm in lieu of an oath that I prepared the submitted dissertation independently and without illicit assistance from third parties, that I appropriately referenced any text or content from other sources, that I used only literature and resources listed in the dissertation, and that the electronic (PDF) and printed versions of the dissertation are identical.

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Place, Date

Signature

*For Mum*

1962

*For Dad*

1960 - 2022

# Acknowledgements

Writing these very last lines of my doctoral thesis feels incredibly surreal. The past four and a half years have been an emotional rollercoaster ride. About a year after I started my PhD project, the pandemic hit and brought the world to a standstill, not only having a massive impact on my scientific progress but also on my mental well-being. Being stuck in home office for almost two years was nothing I had envisioned when I started. I had to say my farewells to dear loved ones and learn how to deal with my grief while still progressing with this work. But just as life leads to farewells, it also ushers in new beginnings. I had the wonderful pleasure of welcoming new people into my life, and in particular, a little incredibly funny human being. I am very grateful for being a part of their lives. They ground me and keep me going.

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Last but not least, T. It feels as though I've known you since kindergarten, and in a way, I suppose I have. Getting to know you more and more these last couple of years brings me so much joy. You saved me and helped shape the person I have always been. This thesis would not have been possible without you. It is your merit, as it is mine.

Dad, I will meet you by the sea.

# Summary

The significance of the marine realm in the context of climate change has prompted extensive research. Oceans play a vital role in regulating Earth's climate, housing a substantial portion of the global biodiversity, and are already affected by anthropogenic climate change. The response of marine species to these shifts may involve geographic range shifts, phenology changes, or adaptation. While anthropogenic climate change looms as a major threat over the marine realm, other human-induced stressors such as pollution, overexploitation, habitat destruction, excessive nutrient run-off from land, and the introduction of invasive species also impact marine ecosystems. Complex feedback mechanisms between these stressors and the marine realm make it challenging to predict the consequences of future climate change accurately.

Marine plankton, a key component for marine ecosystem functioning, are an ideal group to study the response to climate change due to their short life cycles, high reproduction rates, global distribution, and tight coupling to environmental change. Detectable responses to ongoing climate change have been observed in observational data of many marine plankton groups. However, these observations primarily capture small-scale changes due to their limited time frame, necessitating broader analyses for a comprehensive understanding of long-term biodiversity shifts in marine plankton.

This cumulative doctoral thesis aims to comprehensively assess the long-term response of marine plankton biodiversity to climate change, comparable in magnitude to predicted future warming. For this, the fossil record of planktonic foraminifera, prolific marine calcifier, is analysed across the last ice age to the current warm period on global and local scales and compared to changes in reconstructed sea surface temperature (SST). Since the species composition of planktonic foraminifera is mainly predicted by sea surface temperature, the biodiversity change of this group since the last ice age should reflect changes in SST. If other forcing factors play a role, the planktonic foraminifera assemblage change should reveal a response that is not always in pace with the temperature change. By comparing the results with coccolithophore and dinoflagellate responses, two groups representing different functional groups, it is further assessed whether the response of planktonic foraminifera is representative of marine plankton.

Asymmetric range shifts and poleward migrations of planktonic foraminifera assemblages are observed, leading to a surplus of species in the mid-latitudes and the emergence of novel assemblages with the beginning of the current warm period. Deviations between assemblage changes and SST changes during the current warm period are also evident in coccolithophores and dinoflagellates. This suggests the influence of other forcing factors such as ecological interactions in marine plankton responses, especially during periods of lower environmental forcing (i.e., the Holocene). This is highlighted by some evidence for a change in the relationship of planktonic foraminifera and SST since the last ice age. Furthermore, local patterns of biodiversity change revealed potential inaccuracies in the SST reconstruction employed in the study to reflect true SST variations during the current warm period.

In conclusion, this doctoral thesis sheds light on the complex dynamics of marine plankton biodiversity in response to climate change. It highlights the need for a critical evaluation of SST reconstructions before applying them to predict biodiversity change or test ecological concepts, as these are always conditional on the assumption that the used SST accurately reflects true SST. Furthermore, while this study offers insights into the response of plankton communities to climate change similar in magnitude to projected future warming, the accelerated pace of modern global warming raises questions about whether these communities will respond similarly.

# Zusammenfassung

Die Bedeutung der Meere im Zusammenhang mit dem Klimawandel hat zu umfangreichen Forschungsarbeiten geführt. Die Ozeane spielen eine entscheidende Rolle bei der Regulierung des Erdklimas, beherbergen einen erheblichen Teil der globalen Artenvielfalt und sind bereits vom anthropogenen Klimawandel betroffen. Die Reaktion der marinen Arten auf diese Veränderungen kann eine Verlagerung des geografischen Verbreitungsgebiets, eine Veränderung der Phänologie oder eine Anpassung sein. Während der vom Menschen verursachte Klimawandel eine große Bedrohung für die Meere darstellt, wirken sich auch andere vom Menschen verursachte Stressfaktoren wie Verschmutzung, Übernutzung, Lebensraumzerstörung, übermäßiger Nährstoffeintrag vom Land und die Einschleppung invasiver Arten auf die Meeresökosysteme aus. Komplexe Rückkopplungsmechanismen zwischen diesen Stressoren und der Meeresumwelt machen es schwierig, die Folgen des künftigen Klimawandels genau vorherzusagen.

Meeresplankton, eine Schlüsselkomponente für das Funktionieren mariner Ökosysteme, ist aufgrund seiner kurzen Lebenszyklen, seiner hohen Reproduktionsraten, seiner globalen Verbreitung und seiner engen Kopplung an Umweltveränderungen eine ideale Gruppe zur Untersuchung der Reaktion auf den Klimawandel. In Beobachtungsdaten vieler mariner Planktongruppen wurden nachweisbare Reaktionen auf den Klimawandel beobachtet. Aufgrund ihres begrenzten Zeitrahmens erfassen diese Beobachtungen jedoch in erster Linie kleinräumige Veränderungen. Für ein umfassendes Verständnis der langfristigen Veränderungen der biologischen Vielfalt im Meeresplankton sind daher umfassendere Analysen erforderlich.

Diese kumulative Doktorarbeit zielt darauf ab, die langfristige Reaktion der biologischen Vielfalt des Meeresplanktons auf den Klimawandel umfassend zu bewerten, und zwar in einer Größenordnung, die mit der vorhergesagten künftigen Erwärmung vergleichbar ist. Zu diesem Zweck werden die fossilen Aufzeichnungen von planktonischen Foraminiferen, produktiven marinen Kalkbildnern, von der letzten Eiszeit bis zur aktuellen Warmzeit auf globaler und lokaler Ebene analysiert und mit den rekonstruierten Veränderungen der Meeresoberflächentemperatur verglichen. Da die Artenzusammensetzung der planktonischen Foraminiferen hauptsächlich durch die Meeresoberflächentemperatur vorhergesagt wird, sollte die Veränderung der Artenvielfalt dieser Gruppe seit der letzten

Eiszeit Veränderungen der Temperatur widerspiegeln. Wenn andere Einflussfaktoren eine Rolle spielen, sollte die Veränderung der planktonischen Foraminiferenvergesellschaftungen eine Reaktion zeigen, die nicht immer mit der Temperaturänderung übereinstimmt. Durch den Vergleich der Ergebnisse mit den Reaktionen von Coccolithophoriden und Dinoflagellaten, zwei Gruppen, die unterschiedliche Funktionsgruppen repräsentieren, wird weiter geprüft, ob die Reaktion der planktonischen Foraminiferen repräsentativ für das marine Plankton ist.

Asymmetrische Verschiebungen des Verbreitungsgebiets und polwärts gerichtete Wanderungen von planktonischen Foraminiferenvergesellschaftungen werden beobachtet, was zu einem Überschuss an Arten in den mittleren Breiten und dem Auftauchen neuer Vergesellschaftungen mit Beginn der derzeitigen Warmzeit führt. Abweichungen zwischen den Veränderungen in den Vergesellschaftungen und den Temperaturänderungen während der derzeitigen Warmzeit sind auch bei Coccolithophoriden und Dinoflagellaten zu beobachten. Dies deutet auf den Einfluss anderer Einflussfaktoren wie ökologische Wechselwirkungen auf die Reaktionen des marinen Planktons hin, insbesondere in Zeiten mit geringeren Umwelteinflüssen (d. h. im Holozän). Dies wird durch einige Hinweise auf eine Veränderung der Beziehung zwischen planktonischen Foraminiferen und der Meeresoberflächentemperatur seit der letzten Eiszeit unterstrichen. Darüber hinaus haben lokale Muster der Biodiversitätsveränderung mögliche Ungenauigkeiten in der Temperaturrekonstruktion offenbart, die in der Studie verwendet wurde, um die tatsächlichen Temperaturschwankungen während der derzeitigen Warmzeit widerzuspiegeln.

Zusammenfassend lässt sich sagen, dass diese Doktorarbeit die komplexen Dynamiken der biologischen Vielfalt des Meeresplanktons als Reaktion auf den Klimawandel beleuchtet. Sie unterstreicht die Notwendigkeit einer kritischen Bewertung von Temperaturrekonstruktionen, bevor diese zur Vorhersage von Veränderungen der biologischen Vielfalt oder zur Prüfung ökologischer Konzepte verwendet werden, da diese immer von der Annahme abhängig sind, dass die verwendete Temperaturrekonstruktionen die wahre Temperatur genau widerspiegeln. Darüber hinaus bietet diese Studie zwar Einblicke in die Reaktion von Planktongemeinschaften auf einen Klimawandel, der in seiner Größenordnung mit der prognostizierten künftigen Erwärmung vergleichbar ist, doch wirft das beschleunigte Tempo der heutigen globalen Erwärmung die Frage auf, ob diese Gemeinschaften in ähnlicher Weise reagieren werden.

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# Acronyms

| | |
|---|---|
| **DCA** | detrended correspondence analysis |
| **DCA1** | first detrended correspondence axis |
| **ENS** | effective number of species |
| **GAM** | generalised additive model |
| **LDG** | latitudinal diversity gradient |
| **LGM** | Last Glacial Maximum |
| **LOESS** | locally estimated scatterplot smoothing |
| **M-H** | Morisita-Horn index |
| **MAT** | Modern Analogue Technique |
| **PC** | principal component |
| **PC1** | first principal component |
| **PCA** | principal component analysis |
| **RGB** | red, green and blue |
| **SST** | sea surface temperature |
| **WA-PLS** | Weighted Averaging Partial Least Square |

# 1

# Introduction

The marine realm has become a central focus of environmental research, given its immense significance in the context of climate change. Oceans play a pivotal role in regulating Earth's climate, acting as a net sink for heat and carbon dioxide today (Friedlingstein et al., 2022; IPCC, 2023), while also harbouring a substantial portion of the world's biodiversity. Anthropogenic climate change is already having a noticeable impact on marine biodiversity (Antão et al., 2020) and future climate projections indicate even more pronounced effects (Beaugrand et al., 2015; García Molinos et al., 2016; Nolan et al., 2018). To avoid extinction, marine species may respond to these changes by dispersal (i.e., geographic range shifts), changes in phenology (i.e., timing of seasonal activities), or adaptation to new conditions through genetic changes or behavioural adjustments (Munday et al., 2013; Poloczanska et al., 2013). Moreover, species responses might be delayed (Jackson and Sax, 2010) and changes may also occur due to stochasticity in assemblages (i.e., neutral drift; Vellend, 2010), further complicating predictions.

Marine plankton are an ideal group to study when investigating the impact of future global climate change on the marine realm. As a key component of marine ecosystems, marine plankton play a fundamental role in primary production, nutrient and carbon dioxide cycling, and form the basis of the trophic food web. In comparison to other marine organisms, marine plankton have short life cycles and high reproduction rates, thus, plankton dynamics might be tightly coupled to environmental change (Hays et al., 2005). The species composition and biogeography of many marine plankton groups are sensitive to sea surface temperature (SST; Esper and Zonneveld, 2002; Morey et al., 2005; Mohan et al., 2008; Taylor et al., 2008; O'Brien et al., 2016; Hohmann et al., 2020; Rillo et al., 2021), leading to strong latitudinal diversity gradients (LDG; Rutherford et al., 1999; Tittensor et al., 2010; Yasuhara et al., 2012b; Fenton et al., 2016b; O'Brien et al., 2016; Yasuhara et al., 2020b). The LDG is the unimodal decline of species richness from the tropics towards the poles, though many open ocean species show a bimodal pattern with diversity peaks between 20° and 40° north and south of the equator (Figure 1-1; Tittensor et al., 2010).

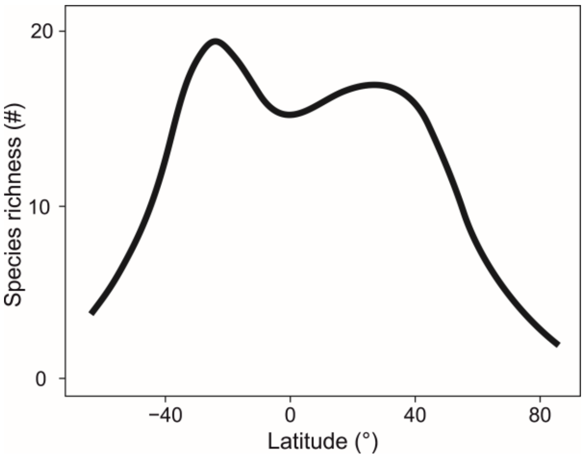

**Figure 1-1:** Latitudinal diversity gradient of planktonic foraminifera showing the bimodal pattern of biodiversity with peaks between 20° and 40° north and south of the equator. After Yasuhara et al., 2020b)

Although anthropogenic climate change is the most significant threat for the marine realm (IPCC, 2023), it is not the sole concern. Other human-induced stressors, such as pollution, overexploitation, habitat destruction, excessive nutrient run-off from agriculture or sewage discharge, and the introduction of invasive species through shipping, pose significant threats (Maxwell et al., 2016), leaving no area of marine ecosystems unaffected (Halpern et al., 2008). The complex dynamics and feedback mechanisms between these stressors and marine biodiversity make it challenging to predict the impact that future global climate change will have on the marine realm.

Observational data of marine plankton can improve future predictions by providing insights into current patterns, mechanisms and rates of biodiversity change (Poloczanska et al., 2013; Antão et al., 2020). Moreover, detectable responses of marine plankton groups to ongoing global climate change have been documented in observational records (coccolithophores: Rost and Riebesell, 2004; diatoms and dinoflagellates: Hinder et al., 2012; planktonic foraminifera: Jonkers et al., 2019). However, observational data are restricted by their short temporal scales and rarely exceed more than 100 years (Dornelas et al., 2018), which is too short to provide information on key aspects of the pre-anthropogenic baseline, such as natural variability, long-term effects or recovery dynamics. Only the geological record offers the possibility to assess natural variation of marine biodiversity and its response to climate change that is predicted for the future on longer timescales.

## 1.1 Microfossils in marine sediments: Snapshots of past biodiversity

While the majority of marine plankton is not preserved in the sediment as they consist of soft-bodied groups (Buitenhuis et al., 2013), certain groups from different functional groups produce organic or inorganic skeletons with high fossilisation potential that resist decomposition (see Figure 1-2). Phytoplankton and zooplankton groups are capable of producing microfossils. The main phytoplankton groups that produce microfossils are diatoms, producing silica shells, coccolithophores, producing mineral exoskeletons (coccospheres) that are composed of several minute plates of calcium carbonate, and some dinoflagellates. Living dinoflagellates, a diverse group of auto-, mixo- and heterotrophic species, are not fossilisable but about 13 % to 16 % produce organic-walled resting cysts that are preserved in the sediment (Head, 1996). Among the microfossils producing zooplankton are radiolarians, forming intricate silica skeletons, planktonic foraminifera, producing calcium carbonate shells, and pteropods that produce delicate aragonite shells.

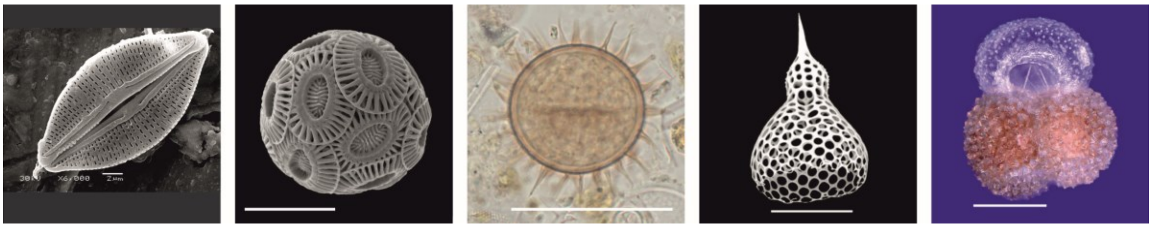

**Figure 1-2:** A collection of microfossils that are produced by certain marine plankton groups. From left to right: diatom frustule (2 µm) © Berezonska, coccosphere of the coccolithophore *Emiliania huxleyi* (3 µm) © Jeremy Young, dinoflagellate cyst (50 µm) © Karin Zonneveld, skeleton of a radiolaria (50 µm; Sandin et al., 2018), and a test of the planktonic foraminifera *Globigerinoides ruber ruber* (100 µm; Lessa et al., 2020). Lengths of scale bars are given in brackets

Due to the global distribution of many of these marine plankton groups and the mostly high preservation potential of their microfossils in marine sediments, the sedimentary record of microfossils provides a comprehensive snapshot of past marine ecosystems, spanning millions of years (Raffi et al., 2006). Serving as reliable indicators of living assemblages (e.g., Kidwell, 2001; Tomašových and Kidwell, 2009; Yasuhara et al., 2012a), microfossils enable the study of past biodiversity changes in response to climate change (Yasuhara et al., 2020a). Moreover, many plankton groups that produce microfossils have been proven to be sensitive to ongoing climate change (coccolithophores: Rost and Riebesell, 2004; diatoms and dinoflagellates: Hinder et al., 2012; planktonic foraminifera: Jonkers et al., 2019). Hence, the marine microfossil record offers insights about the mechanisms and timescales at which marine plankton respond to climate change. The transition from the last cold stage to the current warm period represents a suitable time period for such investigations, because it comprises a comparable magnitude of climate change that is predicted for future global warming, albeit at a different rate (Figure 1-3). Notably, during the last deglaciation (approximately 10,000-17,000 years ago), sea surface temperatures increased by approximately 7 °C, a warming that parallels predictions for 2100 under RCP 8.5 (IPCC, 2023).

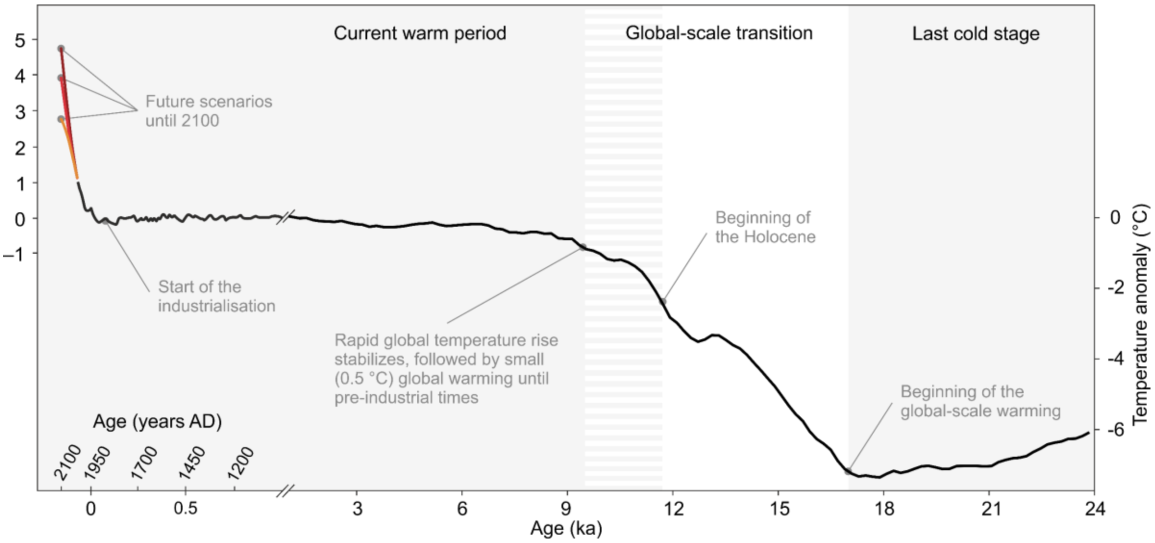

**Figure 1-3:** Sea surface temperature curve covering the transition from the last ice age over the last deglaciation to the current warm period (black line; after Osman et al., 2021). Future warming scenarios representing a warming until 2100 of 3°C, 4°C and more than 4°C since the onset of the industrialisation are indicated as coloured lines (orange, red and dark red; after IPCC, 2023). Temperature anomaly is given relative to the preindustrial last millennium average (1000-1850 AD).

## 1.2 From ancient oceans to modern archives - A short history of marine sediment records and curated microfossil syntheses

Marine sediments are an archive of past marine environments and an essential tool to study Earth's history. Moreover, marine sediments can contain microfossils from marine plankton, informing us about past biodiversity changes. Since the pioneering ocean expeditions of the HMS Beagle (1831–1836), HMS Challenger (1872–1876) and the Albatross (1947–1948), numerous marine sediment records have been retrieved from research expeditions, particularly deep-sea sediment coring programs (Berger, 2011). Scientific ocean drilling commenced in the late '60s with the Deep Sea Drilling Project, active from 1968 to 1983, and followed by subsequent drilling programs and culminating in the current International Ocean Discovery Program in 2013 (htttp://deepseadrilling.org/about.htm). These ocean drilling projects have contributed to over 11,000 peer-review publications on a global scale (Clement and Malone, 2019; Koppers et al., 2019). Consequently, a wealth of marine data and data on marine microfossils is available through open data sharing, with dedicated public repositories such as PANGAEA (https://www.pangaea.de/; Felden et al., 2023) and NOAA's World Data Service for Paleoclimatology (https://www.ncei.noaa.gov/products /paleoclimatology).

Still, microfossil data from different studies and repositories can be vast and scattered, making data comparisons challenging. Thanks to collaborative effort, these microfossil datasets have been partially compiled in curated and taxonomically harmonised syntheses, allowing easier examination of larger patterns on various spatial and temporal scales. The early syntheses relied on the laborious manual compilation of microfossil data from the literature, with the history of microfossil data synthesis dating back to the 1970s and 1980s with the CLIMAP project that aimed to map the climate state during the Last Glacial Maximum (CLIMAP Project Members, 1976, 1981). Another notable synthesis, the NSB database (for Neptune Sandbox Berlin), initiated in 1998 as the Paleobiology Database and continuously developed for the past 25 years, compiles global microfossil data from deep sea drilling cores and contains over one million records (Lazarus, 1994; Renaudie et al., 2020). Additionally, the MARGO data synthesis, published in 2005, aimed to reconstruct SST and sea-ice extent of the glacial ocean (Kucera et al., 2005a). ForCenS, an update of MARGO, serves as a valuable calibration dataset for palaeoclimate reconstructions (Siccha and Kucera, 2017). A recent noteworthy addition to the microfossil data synthesis is Triton (Fenton et al., 2021), encompassing over 500,000 spatiotemporal records of planktonic foraminifera occurrences. It is essential to note that this overview of microfossil data synthesis is not exhaustive but aims to showcase the extensive history of ongoing development of these valuable syntheses.

## 1.3 State of the art & research gaps in biodiversity change research using the sedimentary record of marine plankton

Many studies investigating the sedimentary record of marine microfossils have one thing in common: they either focus on the temporal patterns of single or few locations, or on the spatial pattern of individual time slices. The latter approach has been successfully used to reconstruct past global climate change (e.g., de Vernal et al., 2005; Gersonde et al., 2005; Kucera et al., 2005a; Kucera et al., 2005b). However, the potential of the fossil record of marine plankton to unveil biodiversity changes across time periods of environmental change comparable to expected future climate change remains relatively unexplored.

The extensive efforts in compiling curated and globally consistent databases, such as the most recent Triton database (Fenton et al., 2021), have opened up possibilities for spatio-temporal cross-scale analysis of marine plankton. For instance, it has recently been shown how the latitudinal diversity gradient of planktonic foraminifera has developed over the past 40 million years (Fenton et al., 2023) and how the species richness of planktonic foraminifera has changed in response to temperature changes over the last 8 million years (Woodhouse et al., 2023). These studies investigated speciation, extinctions, and species richness changes of marine plankton on long time scales. However, biodiversity encompasses more than species richness, as it can also be influenced by dominance shifts or the species replacements without necessarily altering species richness (Hillebrand et al., 2018). Additionally, biodiversity patterns are timescale-dependent as highlighted by Lewandowska et al. (2020). On long time-scales spanning millions of years, biodiversity is partly driven by speciation and extinction processes, while on shorter timescales, spatial species redistributions in response to climate change are more significant drivers of biodiversity patterns.

Hence, assemblage change in marine ecosystems plays a critical role in shaping ecosystem functioning across various timescales. On shorter timescales, for instance, geographical species range shifts can lead to novel assemblage (Poloczanska et al., 2013; García Molinos et al., 2016; Antão et al., 2020), altering ecological interactions and trophic food webs, potentially leading to cascading effects. Furthermore, assemblage changes that reduce biodiversity may result in ecosystem instabilities, and assemblage change can be delayed, leading to a mismatch between species response and their changing environment. Consequently, investigating biodiversity changes that occur before species extinctions is crucial for a comprehensive understanding of the potential impact of predicted future climate change on the marine realm.

Nonetheless, spatio-temporal cross-scale analyses investigating biodiversity changes that go beyond simple species richness are currently scarce but offer vital insights to the response of marine plankton to climate change. For instance, Jonkers et al. (2019) demonstrated that modern plankton are already affected by anthropogenic climate change through a comparison of observational sediment trap data with pre-industrial sediment samples. Similarly, Yasuhara et al. (2020b) revealed that the tropical decline observed in many marine plankton groups is not a recent phenomenon but likely emerged around 15 thousand years ago by comparing pre-industrial sediment samples with sediment samples from the Last Glacial Maximum (LGM).

In conclusion, spatio-temporal biodiversity studies currently rely on species richness as a biodiversity index or on comparing distinct time slices due to limited data availability on a larger scale. What is missing are continuous spatio-temporal cross-scale analyses that explore biodiversity change beyond species richness across time periods of environmental change that is comparable to the predicted future warming. This is the research area where this study finds its significance.

## 1.4 Thesis objectives

This thesis aims to assess the long-term response of marine plankton biodiversity to climate change that is comparable in magnitude to expected future warming. To achieve this, sediment records of planktonic foraminifera from the North Atlantic Ocean are utilised and assemblage composition changes from the last cold stage to the current warm period are investigated. Due to their high dispersal in an environment with fewer physical barriers than in the terrestrial realm, marine plankton often respond to such environmental changes through range shift (Poloczanska et al., 2013; Lenoir et al., 2020). These range shifts may proceed at different paces among species and, in fact, asymmetries between the trailing and leading edge of species range shifts have been observed in marine plankton groups, leading to the emergence of novel assemblages (Poloczanska et al., 2013; García Molinos et al., 2016). The species composition of planktonic foraminifera is mainly affected by SST changes (Morey et al., 2005; Rillo et al., 2021) and although these asymmetric range shifts might be induced by single environmental forcing factors, migrating species will experience novel direct and indirect ecological interactions with other species that did not occur in their original habitat. Therefore, range shifts driven by changes in abiotic conditions are probably modified by ecological complexity (Van der Putten et al., 2010).

The planktonic foraminifera time series used throughout this thesis cover the entire latitudinal gradient of the North Atlantic Ocean, which is intricately connected to the global climate system. Thus, it is reasonable to expect that variations in the planktonic foraminifera assemblages in the North Atlantic will align with broader global climate changes. Consequently, if planktonic foraminifera predominantly respond to climate change through temperature-driven range shifts, the overall planktonic foraminifera assemblage change from the last cold stage to the current warm period in the North Atlantic Ocean should correspond to changes in global mean SST. However, if other forcing factors, such as ecological interactions, also come into play, the planktonic foraminifera assemblage change should reveal a response that is not always in pace with the environmental forcing. This first hypothesis (H1) is tested by comparing the overall assemblage change in the North Atlantic Ocean over the past 24 thousand years (kyr) from the last cold stage to the current warm period with global mean SST. Additionally, assessing the individual time series will allow a closer evaluation of the time of the tropical diversity decline observed by Yasuhara et al. (2020b).

**H1: Planktonic foraminifera assemblage change is in equilibrium with SST change**

To assess if the overall response of planktonic foraminifera to the climate change of the past 24 kyr is representative of marine plankton, a comparison with other functional plankton groups is essential. By incorporating coccolithophores and dinoflagellates into the analysis, the dataset encompasses marine plankton with varying diversity, trophic strategies, ecological importance, and function. As the species composition of these groups is also primarily affected by SST, along with other environmental factors such as light availability, productivity and nutrient availability (Esper and Zonneveld, 2002; Mohan et al., 2008; Taylor et al., 2008; Chen et al., 2011a; Charalampopoulou et al., 2016; O'Brien et al., 2016; Hohmann et al., 2020), we expect comparable responses, leading to the formulation of the second hypothesis:

**H2: The response of phytoplankton and zooplankton to SST change is comparable**

The first part of this thesis resulted in a surprising observation: assemblage change of planktonic foraminifera, coccolithophores, and dinoflagellate cysts continued for several thousand years into the current warm period, thus postdating the last deglaciation. This prolonged change occurred despite the comparably low temperature forcing during the current warm period. This observation was made by comparing the overall plankton change in the North Atlantic Ocean to global mean SST. Even though the overall plankton change should align with broader climate signals, it is evident that overall observed assemblage change in the North Atlantic is the result of local-scale changes reflecting local rather than global mean SST. Consequently, to gain more comprehensive understanding, it is essential to examine the plankton response to SST changes on a local scale, particularly considering spatial variations in predicted future warming (IPCC, 2023). For this purpose, local planktonic foraminifera assemblage time series are compared with their respective local SST to test the third hypothesis (H3):

**H3: Local SST change explains more variance in planktonic foraminifera assemblage change than global SST**

Alongside the scientific objective of this thesis, which aims to assess the long-term response of marine plankton biodiversity to climate change that is comparable to predicted future warming, an underlying goal is to make most use of the publicly available assemblage datasets that are stored in repositories. To achieve this, all available assemblage time series that met the data requirements of this thesis were identified. Since these time series were initially compiled by different researchers, taxonomic harmonisation and consistency checks were necessary for a comprehensive spatial-temporal analysis of the data.

However, data standardisation is often hindered by the complexity of biological nomenclature and the use of different classification criteria for specimens, leading to numerous challenges and problems during taxonomical data harmonisation. Mapping these problems helps to identify group-specific species complexes that are difficult to harmonise, as well as general issues encountered during data standardisation. This valuable information can then be used to inform community-derived (meta)data standards and develop pipelines for automated taxonomical data harmonisation. Consequently, an additional objective (O1) of this thesis is:

**O1: Mapping the common problems and challenges associated with the taxonomic harmonisation of planktonic foraminifera assemblage datasets**

## 1.5 Material and approach

This Chapter provides a short overview of the materials and general approach that was followed in this thesis, along with a rationale for their selection. To avoid redundancy, the reader is directed to the relevant Chapters for more detailed explanations of the material and specific methods used. Throughout this thesis, the terms “assemblage” and “community” are used as defined in Fauth et al. (1996), with “community” referring to all the species that occur in the same place at the same time and "assemblage" referring to all taxa of phylogenetically related groups within a community. Throughout this thesis, age information is presented as kyr (referring to time periods) and ka (referring to specific dates), with 0 ka denoting the 1950 Common Era.

### 1.5.1 Assemblage data

This thesis primarily relies on the sedimentary record of planktonic foraminifera, a group of prolific marine calcifying zooplankton with global distribution that inhabits the upper ocean layers and serves as an important palaeoceanographic indicator. Planktonic foraminifera have one of the most comprehensive fossil records (Aze et al., 2011) and a large amount of publicly archived datasets is available. Since planktonic foraminifera species composition is mainly influenced by SST (Morey et al., 2005; Rillo et al., 2021), these archived datasets have often been used to reconstruct past climate (e.g., Kucera et al., 2005a; Kucera et al., 2005b) and to study biogeographic patterns and their relationship to past climate (Ezard et al., 2011; Yasuhara et al., 2012b; Fenton et al., 2016a; Yasuhara et al., 2020b). However, due to their excellent fossil record, standardised taxonomy and the existence of abundantly available data, planktonic foraminifera also make an ideal group to study the long-term response of marine plankton to past climate change. This study specifically focuses on the North Atlantic Ocean due to the extensive availability of publicly accessible datasets and to ensure best possible spatial coverage of time series.

The planktonic foraminifera assemblage count time series used in this thesis cover the time period from the last cold stage across the last deglaciation to the current warm period, encompassing the past 24 kyr. This period is particularly suitable as it represents a climatic upheaval comparable to the predicted future global warming extent (Figure 1-3; Jackson and Overpeck, 2000). It is also a time period where most data are available at high resolution (less than 1 kyr) and with reliable age information. To compare the response of the planktonic foraminifera with marine phytoplankton groups, additional datasets have been compiled for coccolithophores and organic-walled dinoflagellate cysts, covering the same spatial and temporal extent. Due limited availability of suitable data for these groups, the compiled phytoplankton datasets are notably smaller than the planktonic foraminifera dataset. For a more extensive description of planktonic foraminifera and the compilation and harmonisation of the planktonic foraminifera dataset, please refer to Chapter 3 and for more information on coccolithophores and dinoflagellates and the compilation and harmonisation of the corresponding datasets, please refer to Chapter 4.

### 1.5.2 Measure of climate change

In this study, SST serves as a measure of climate change, as it significantly influences planktonic foraminifera assemblage change (Morey et al., 2005; Rillo et al., 2021). Since direct measurements of the true SST of past time periods are unavailable, past biodiversity changes in response to climate change rely on inferred or reconstructed SST. Various proxies, such as Ma/Ca ratios of foraminiferal shells (Rosenthal et al., 1997), oxygen isotopic composition of foraminiferal shells (Shackleton, 1974), alkenones in coccolithophores (Prahl et al., 1988), and coral growth bands (Lough and Barnes, 2000) are related to past SST changes. Additionally, the assemblage composition of specific microfossils (e.g., dinoflagellate cysts, planktonic foraminifera. and diatoms) and pollen can be directly translated into past SST using modern analogue techniques or transfer functions (e.g., de Vernal et al., 2005; Gersonde et al., 2005; Kucera et al., 2005b; Hohmann et al., 2020). Furthermore, climate models simulate past SST and reanalyses combine model simulations with proxy data reconstructions to further refine the modelled past SST.

In this study, independent mean annual SST from the Last Glacial Maximum reanalysis (LGMR; Osman et al., 2021) were utilised because of their local availability for all time series and availability as global mean SST. Although alternative SST proxy reconstructions (e.g., SST inferred from Mg/Ca, alkenones, or oxygen isotopes) are independent from assemblage composition (unlike transfer functions and analogue techniques), they were not utilised because they were only available for a subset of time series. For a more comprehensive explanation of the SST measure used in this study, please refer to Chapter 4.

# 2 Outline of manuscripts and own contribution

This thesis is a culmination of four manuscripts in all stages of publication written over the course of four and a half years. Each paper is outlined below with a short summary, the authors contributions and my detailed own contribution. To minimize redundancy, references have been removed from each manuscript and are cited in a single reference list at the end of this thesis (see References).

## 2.1 Manuscript I: Plankton response to global warming is characterized by non-uniform shifts in assemblage composition since the last ice age

**T. Strack, L. Jonkers, M.C. Rillo, H. Hillebrand, and M. Kucera**

Published in *Nature Ecology & Evolution* 6(12), 1871-1880 (2022) and available at DOI: 10.1038/s41559-022-01888-8.

### Short summary

This study examines the response of planktonic foraminifera biodiversity to past climate changes similar in magnitude to future global warming. Using fossil records, we found that as temperatures rose after the last cold stage, planktonic foraminifera assemblages shifted and continued changing until about 5 ka ago, despite relatively stable global temperatures in the current warm period. The response was most significant in mid-latitudes, involving range expansion and emergence of novel. The findings suggest that past climate change led to the establishment of new assemblages, implying that ongoing anthropogenic warming could also result in novel and distinct plankton community compositions.

### Author contribution

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. and M.C.R.. All authors interpreted and discussed the results and contributed to the writing and editing of the manuscript.

## Detailed own contribution

For this study, I searched the literature and public data repositories for extant planktonic foraminifera assemblage count data with a main focus on PANGAEA. Out of the initially 257 identified records, I then identified the records that were situated in the North Atlantic Ocean and adjacent seas and that contained data from the past 24 kyr. From the remaining records, I removed all records that did not fit my study requirements (i.e., full assemblage counted, full time period covered with a resolution of smaller than approximately 1 kyr), leaving me with 25 records for which I compiled all metadata necessary for my study (i.e., reference and data link, location, water depth, metadata on the counting, information on age model). For some of these records the data were not yet publicly available, so I got in contact with the authors to get it. For the 16 records that were not included in the PALMOD 130k marine palaeoclimate data synthesis V1.1 (Jonkers et al., 2020), I revised the age models in PaleoDataView using the approach of Jonkers et al. (2020).

As a next step, I manually screened all datasets and checked for inconsistencies and plausibility. I compiled a dictionary of taxa synonyms and wrote an R script for loading the data, taxonomic harmonisation and compilation of a final assemblage data set containing all necessary (meta)data. For the LGM reference dataset, I updated a subset of the MARGO dataset with samples from my compilation that were not included.

I conducted all the analyses and wrote the main parts of the R code for the analyses and plotting the figures, with some helps from L.J. and M.C.R. with specific coding problems. After discussing all results in close collaboration with all co-authors, I finalised the figures and prepared the first draft of the manuscript, and revised and included remarks from all co-authors in the internal revision processing. Finally, I submitted the paper to Nature Ecology & Evolution, and led the submission process. In particular, this includes correspondence with the editors, directing the internal revision process with the co-authors, and writing the response letter to the reviewer in close consultation with the co-authors, leading to the final publication of our first manuscript in Nature Ecology & Evolution.

## 2.2 Manuscript II: Coherent response of zoo- and phytoplankton assemblages to global warming since the last ice age

**T. Strack, L. Jonkers, M.C. Rillo, K.-H. Baumann, H. Hillebrand, and M. Kucera**
Submitted to *Global Ecology and Biogeography* in 2023

### Short summary

This research investigates how the biodiversity of marine plankton groups responded to past climatic changes comparable to projected future warming. The study covers the past 24 kyr, analysing plankton assemblages including foraminifera, dinoflagellates, and coccolithophores in the North Atlantic Ocean. Results indicate that all three groups experienced similar biodiversity changes, with shifts starting around 16-17 ka ago and continuing through the current warm period until about 4-5 ka ago. This extended period of change suggests significant ecological reshuffling and a potential shift in dominant drivers of plankton assemblage change. The findings highlight the potential long-term impacts of future global warming on marine plankton communities.

### Author contribution

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. contributed the coccolithophore assemblage counts. All authors interpreted and discussed the results, and contributed to the writing and editing of the manuscript.

### Detailed own contribution

For this study, I expanded the compilation of planktonic foraminifera assemblage records by incorporating assemblage count data from organic-walled dinoflagellate cysts and coccolithophores using the same approach as in the initial study. The PANGAEA search provided about 30 records that are located in the North Atlantic Ocean and adjacent seas for both plankton groups. After identifying the records that fulfilled the study requirements (i.e., full assemblage counted, full time period covered with a resolution of smaller than approximately 1 kyr), reducing the number to 4 coccolithophore and 6 dinoflagellate cyst records, and compiling the (meta)data, I revised the age models of the remaining records in PaleoDataView using the approach of Jonkers et al. (2020).

I once again reviewed all dataset, ensuring consistency and validity. I updated the taxa synonym dictionary accordingly and modified the R script for the taxonomic harmonisation of these new plankton groups. I conducted all analyses, modifying initial code to accommodate for additional and revised analyses (e.g., generalised additive models, effective number of species). I also wrote new R code for a sensitivity analysis to test address potential sampling bias in the observed plankton signals.

Collaborating closely with the co-authors, I discussed the results in detail and then produced the first draft of the second manuscript. Following an internal review process, I incorporated feedback from all co-authors and submitted the manuscript to Global Ecology and Biogeography. Given that the coccolithophore records are unpublished datasets from co-author K.-H.B., I prepared these datasets for submission to PANGAEA following community data guidelines to facilitate the reusability of these microfossil assemblage datasets.

## 2.3 Manuscript III: Investigating Holocene planktonic foraminifera assemblage change in the North Atlantic Ocean

**T. Strack, L. Jonkers, and M. Kucera**

Manuscript in preparation for submission

### Short summary

To further investigate our initial observation of a prolonged overall planktonic foraminifera assemblage change during the current warm period despite an overall low temperature forcing, this study explores if this response is detectable on the local scale. We do this by comparing planktonic foraminifera assemblage change during the Holocene with local SST. Additionally, we use planktonic foraminifera-derived SST to estimate how much assemblage change could be in theory explained by temperature change assuming uniformitarianism. We find that local SST reconstructions might underestimate true local SST and find evidence that the relationship between planktonic foraminifera assemblage change and SST has changed over the last 24 kyr, confirming our initial findings.

## Authors contribution

All authors jointly contributed to the design and planning of the study. T.S. conducted the data analyses and designed the figures. T.S. wrote the R code with contributions from L.J. All authors interpreted and discussed the results, and contributed to the writing and editing of the manuscript.

## Detailed own contribution

To compared the planktonic foraminifera assemblage dataset with local SST, I downloaded publicly available local LGMR SST data. However, adapting this data posed challenges. I invested significant time troubleshooting the issues and sought help on online programming communities. Ultimately, I identified the problem: the specialized format of the grid, only compatible with specific climate modelling software. I consulted with Matthias Prange, a climate modeller at MARUM, and he converted the grid to a standard latitude-longitude format, enabling me the extraction of local SST time series for the foraminifera records.

I also produced the R code to compute planktonic foraminifer-derived SST using both analogue and transfer function approaches. This involved a subset of the ForCenS calibration dataset with corresponding observed SST from the World Ocean Atlas 1998, provided by L.J. I performed subsequent analyses using R, including linear regression models and Wilcoxon signed rank tests, and developed initial figure plots. After thorough discussion with all co-authors, I refined all figures and drafted the first version of the manuscript. Following an initial internal review, I incorporated feedback from all co-authors to produce this second draft of the manuscript.

## 2.4 Manuscript IV: How to improve the reusability of micropalaeontological assemblage data? (or: Who knows Globorotalia mentum?) - A planktonic foraminifera case study

**T. Strack, L. Jonkers, R. Huber, and M. Kucera**

Manuscript in preparation for submission

### Short summary

Marine microfossil assemblage records offer unique insights into long-term biodiversity shifts not possible with short-term data. Open data sharing aids biodiversity research, yet harmonizing complex taxonomic data remains a challenge. This study underscores challenges that occur while harmonising planktonic foraminifera assemblage data and advocates for community-defined standards to improve data usability. An automated solution for harmonizing existing data on PANGAEA is proposed, along with examples of an ideal dataset.

### Authors contribution

M.K. and R.H. conceived the project idea, and all authors jointly contributed to the design and planning of the project. L.J., T.S. and R.H. conducted the data analyses, L.J. wrote the code for the automated R pipeline and T.S. produced the flowchart explaining the functioning of the R pipeline. All authors interpreted and discussed the results, and contributed to the writing and editing of the manuscript.

### Detailed own contribution

L.J. compiled a list of planktonic foraminifera species names from 2,400 data files retrieved from PANGAEA. I then identified and corrected AphiaIDs that have been wrongly assigned by PANGAEA's automated annotation service. In collaboration with L.J., we mapped the challenges and problems that occur during planktonic foraminifera data harmonisation and identified specific complexes that produce a lot ambiguity. I then developed initial versions of decision trees to resolve these complexes and reduce the ambiguity, which were then discussed with L.J. who translated these into an automated R pipeline. I tested the functioning of the script and created a visual flowchart illustrating the functioning of the pipeline. Additionally, I submitted two new subspecies names to

WoRMS that were previously not incorporated. I produced the initial project draft, incorporating feedback from all co-authors. Finally, I wrote the first draft of this manuscript, outlining common challenges in planktonic foraminifera data harmonisation and ideal dataset criteria, and produced additional figures. After integrating L.J.'s feedback, I finalised the second version of this manuscript.

# 3 Manuscript I

## Plankton response to global warming is characterized by non-uniform shifts in assemblage composition since the last ice age

**T. Strack, L. Jonkers, M.C. Rillo, H. Hillebrand, and M. Kucera**

Published in *Nature Ecology & Evolution* 6(12), 1871-1880 (2022) and available at DOI: 10.1038/s41559-022-01888-8.

### Abstract

Biodiversity is expected to change in response to future global warming. However, it is difficult to predict how species will track the ongoing climate change. Here we use the fossil record of planktonic foraminifera to assess how biodiversity responded to climate change with a magnitude comparable to future anthropogenic warming. We compiled time series of planktonic foraminifera assemblages, covering the time from the last ice age across the deglaciation to the current warm period. Planktonic foraminifera assemblages shifted immediately when temperature began to rise at the end of the last ice age and continued to change until approximately 5,000 years ago, even though global temperature remained relatively stable during the last 11,000 years. The biotic response was largest in the mid-latitudes and dominated by range expansion, which resulted in the emergence of new assemblages without analogues in the glacial ocean. Our results indicate that the plankton response to global warming was spatially heterogeneous and did not track temperature change uniformly over the past 24,000 years. Climate change led to the establishment of new assemblages and possibly new ecological interactions, which suggests that current anthropogenic warming may lead to new, different plankton community composition.

## 3.1 Introduction

Climate change affects biodiversity on multiple time scales. On longer time scales, species may adapt or go extinct. On shorter time scales, climate change will first affect species biogeography, because in the absence of physical barriers, species can respond to change by habitat tracking, a central concept in global change ecology (Brett, 1998; Brett et al., 2007). Range shifts in response to the ongoing global warming have been documented in many species across ecosystems (for reviews see Walther et al., 2002; Root et al., 2003; Parmesan, 2006), but because of the lack of barriers and high dispersal potential due to currents, habitat tracking should be particularly widespread in marine plankton (Poloczanska et al., 2013; Lenoir et al., 2020; Rillo et al., 2021). Although habitat tracking may be induced by a single forcing factor, the migrating species will experience novel direct and indirect ecological interactions with other species that did not occur in their original habitat. Therefore, range shifts driven by changes in abiotic conditions are likely modified by ecological complexity, such as the emergence of new ecological interactions (Van der Putten et al., 2010). Moreover, the ecological niche of a species depends on multiple abiotic parameters, which may not all change at the same pace across space. Therefore, range shifts in response to environmental change may differ among species and proceed at different paces, resulting in the establishment of novel communities that differ from those existing prior to the environmental change. There is indeed evidence for such novelty as we observe asymmetry between the leading and trailing edge of ongoing species expansions (Chen et al., 2011b; Poloczanska et al., 2013; García Molinos et al., 2016; Antão et al., 2020), which creates new assemblages made of expanding species meeting persisting ones. Besides the effects on biodiversity and species richness, asymmetrical range shifts and the resulting novel ecological interactions may also have important consequences for the overall functioning of ecosystems, including effects on trophic interactions, material flow, primary production and biogeochemical cycles (Occhipinti-Ambrogi, 2007; Williams and Jackson, 2007; Beaugrand et al., 2015; Benedetti et al., 2021).

Biological monitoring of biodiversity change can inform us about current patterns (Poloczanska et al., 2013; Antão et al., 2020) and rates (Poloczanska et al., 2013; Burrows et al., 2019) of species response to environmental change. However, such monitoring cannot fully constrain the long-term ecological outcomes of environmental change because it rarely spans more than a century (Dornelas et al., 2018; Antão et al., 2020) and the magnitude of environmental change in many key parameters over the monitored period is small compared to the likely extent of future global change. In many parts of the ocean, however, sedimentary microfossil records of hard-bodied plankton groups are available with resolution sufficient to study biodiversity change across millennia, covering larger magnitudes of environmental change, e.g. the warming associated with the transition from the last ice age to the current warm period (Jonkers et al., 2020). Although the majority of plankton biomass is composed of soft-bodied groups that are not preserved in the fossil record (Buitenhuis et al., 2013), the diversity of marine microfossils correlates globally to overall marine diversity (Yasuhara et al., 2017). Plankton groups with fossil record can therefore serve as a proxy to study plankton biodiversity change in the past and inform us about what to expect in the future. However, their potential to reveal the ecological changes of the planktonic communities on a basin-wide scale during the last climatic upheaval has never been exploited.

One of the most complete microfossil records among marine plankton is that of planktonic foraminifera (Aze et al., 2011), calcifying zooplankton that inhabit the upper water layer of all ocean basins. They interact with other plankton groups through photosymbiosis (Takagi et al., 2019), predation or grazing (Schiebel and Hemleben, 2017). Their spatial distribution and species turnover are sensitive to sea-surface temperature (Morey et al., 2005; Rillo et al., 2021), resulting in a strong latitudinal diversity gradient (LDG; Rutherford et al., 1999; Tittensor et al., 2010; Yasuhara et al., 2012b; Fenton et al., 2016b; Yasuhara et al., 2020b) and a detectable response to the ongoing global warming (Jonkers et al., 2019) which has also been documented in a range of other marine plankton groups (Southward et al., 1995; Beaugrand et al., 2002; Hinder et al., 2012; Burrows et al., 2019). Owing to their excellent fossil record, resolved and standardised taxonomy, and the existence of large datasets initially generated to reconstruct past climate (Kucera et al., 2005a; Kucera et al., 2005b; Siccha and Kucera, 2017; Fenton et al., 2021), the fossil record of planktonic foraminifera has been widely used to investigate long-term changes in marine plankton biodiversity (Ezard et al., 2011; Fenton et al., 2016a; Lowery and Fraass, 2019) and biogeographic patterns (Yasuhara et al., 2012b; Yasuhara et al., 2020b). Since there is no evidence for extinctions or the emergence of new species of planktonic foraminifera in the late Quaternary (Wade et al., 2011) and the thermal niche of the extant species is considered to have been stable over the last glacial cycle (Antell et al., 2021), planktonic foraminifera should have responded to the rapid temperature rise that accompanied the end of the last ice age by habitat tracking, resulting in an immediate and directional response. If planktonic foraminifera species responded predominantly by habitat tracking, the assemblage compositional change should be scaled to the environmental forcing, resulting in the conservation of assemblage composition, which were shifting in pace with the movement of the constituent species. However, if the biotic response involved processes beyond temperature-driven habitat tracking, the fossil record should reveal an ecological response that was not always in pace with the environmental forcing, and potentially the emergence of novel assemblages. Distinguishing between these possible trajectories is important to assess the long-term response of plankton biodiversity to global change.

Here we compile a coherent spatio-temporal dataset of 25 time series of planktonic foraminifera assemblage (sensu Fauth et al., 1996) composition that are distributed along the full latitudinal gradient of the North Atlantic Ocean and span the past 24 thousand years (ka) with an average resolution of 600 years (Figure 3-1a; Extended Data Table 3-1). The time series cover the time from the last ice age across the deglaciation to the present warm period, spanning a climatic upheaval with a magnitude comparable to the likely extent of future global warming (Jackson and Overpeck, 2000). We use global mean surface temperature as a measure of climate change and analyse time series of biodiversity change to explore how the past environmental change related to the observed species redistributions and changes in assemblage composition through time. Our analyses reveal immediate and directional shifts in the distribution of assemblages during the temperature rise that accompanied the end of the last ice age but a large component of the change in assemblage post-dates the rapid deglacial warming and we detect the emergence of novel assemblages during the climatically rather stable current warm period. Remarkably, the rate of community change during the current warm period is as high as during the deglaciation, even though the environmental forcing by global temperature is much weaker.

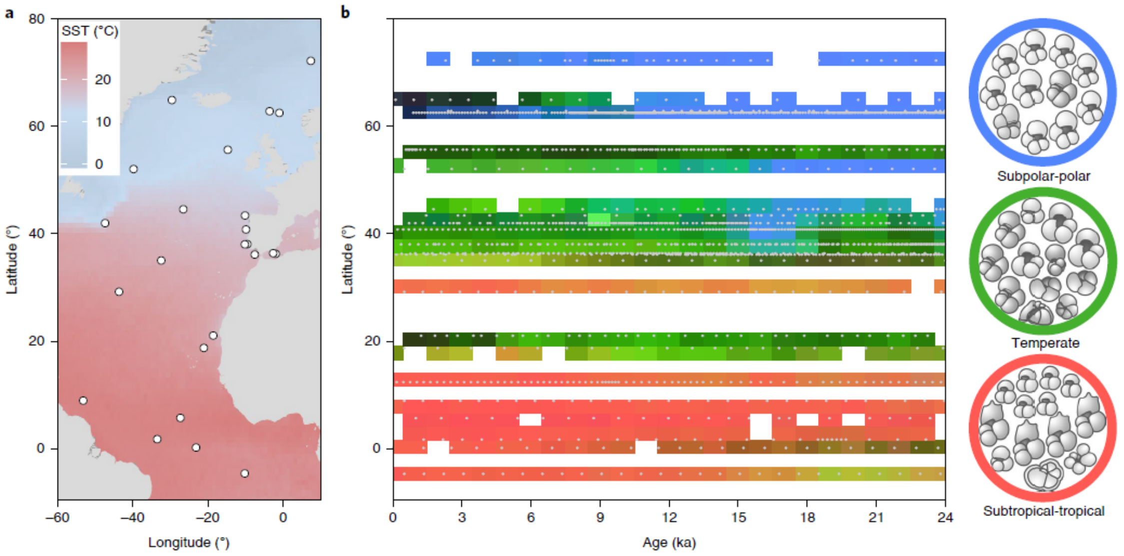

**Figure 3-1:** Transformation of planktonic foraminifera assemblage composition in the North Atlantic since the last ice age. **a**, Location of 25 analysed planktonic foraminifera assemblage time series (white circles). Background: modern annual mean sea-surface temperature (SST) from the WOA18 (Locarnini et al., 2019). **b**, Visualization of the spatio-temporal pattern of the overall assemblage change, with the first three PC of dissimilarity serving as RGB coordinates (see Methods) for each analysed assemblage (grey dots), gridded at 1 kyr by 2.5° latitude. Similar colours in the grid correspond to similar species compositions. The three circles on the right side show exemplary compositions of the three main assemblages visualized in **b**. We are aware that the RGB colour palette is not colour-blind friendly and provide another version of **b** in Extended Data Figure 1.

## 3.2 Results

We analysed 25 time series of planktonic foraminifera abundance data across the latitudinal gradient of the North Atlantic Ocean (Figure 3-1a, Extended Data Table 3-1). The species composition of all samples of this dataset indicated the presence of three main assemblages: subpolar-polar, temperate and subtropical-tropical (Figure 3-1b). Across the last 24 ka, there was a systematic transformation of assemblage composition from colder towards warmer species compositions (Figure 3-1b; Extended Data Figure 3-1). The largest transformation occurred in the mid-latitudes, where subpolar-polar assemblages were replaced by temperate ones over the transition from the last ice age to the current warm period. With the beginning of the current warm period (at around 11 ka), subtropical-tropical assemblages expanded poleward, south and north of the equator (Figure 3-1b). At around 6-9 ka, temperate species migrated poleward to about 65°N. In the mid-latitudes, the prevalence of temperate assemblages was interrupted by a transient emergence of subpolar-polar assemblages at 15-17 ka, associated with a well-known cold period (Heinrich Event) with icebergs reaching south to the Iberian Margin (Ruddiman, 1977; Broecker, 1994; Bard et al., 2000).

The principal component (PC) of assemblage change suggests a unidirectional transformation (Figure 3-2a), with the first PCs of the individual faunal trends explaining 20.4 - 65.3 % of the variance in each time series (Figure 3-2b). Initially, the assemblage composition tracked the global temperature forcing from the last ice age until around 11 ka (Figure 3-2a,c). Then assemblage change seems to decouple from temperature, as the faunal change continued at the same pace for about 6 ka despite a much smaller magnitude of warming during this time (Figure 3-2d).

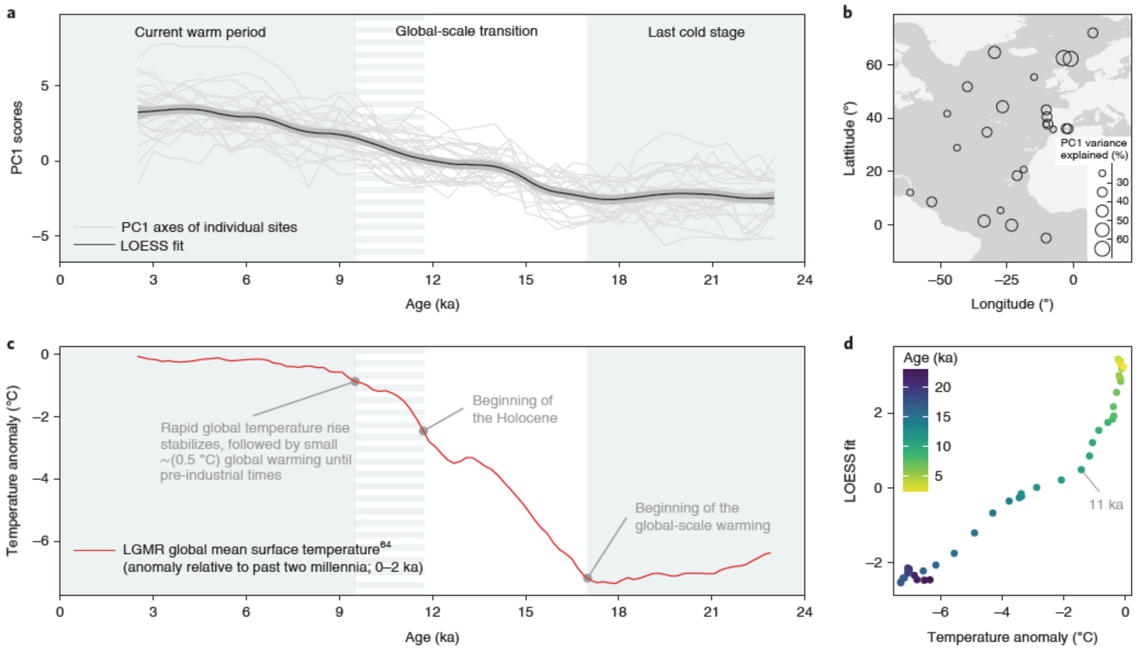

**Figure 3-2:** Planktonic foraminifera assemblage response to global warming during the past 24 kyr. **a**, Compositional change within individual time series shown as first principal component (PC1) axes scores (grey lines, interpolated at 0.5 kyr) and overall compositional change shown as LOESS fit (black line) and its 95% confidence interval (grey shading). **b**, Variance explained by individual PC1 axes at each site. **c**, Development of global mean surface temperature (red line; Osman et al., 2021). The temperature anomaly is referenced to the past two millennia (0–2 ka). **d**, Comparison of overall compositional change (LOESS fit) and global warming (temperature anomaly).

Over the past 24 ka, the largest changes in species richness occurred in the mid-latitudes and richness in the tropics remained unchanged (Figure 3-3a,b). The gains and losses components of the species richness change reveal an asymmetry between local colonizations and extinctions with the magnitude of local colonisation outpacing local extinctions (Figure 3-3c-f). The overall accumulation of species gains (Figure 3-3c) can be attributed to the mid-latitudes where species gains were highest (Figure 3-3d). In contrast, species losses were greatest in the tropics since the last deglaciation but neutral or lower in the mid- and high-latitudes (Figure 3-3f) with an overall lower magnitude (Figure 3-3e). The poleward migration of planktonic foraminifera species into new environments (Figure 3-1b) and the persistence of the original species in these same areas

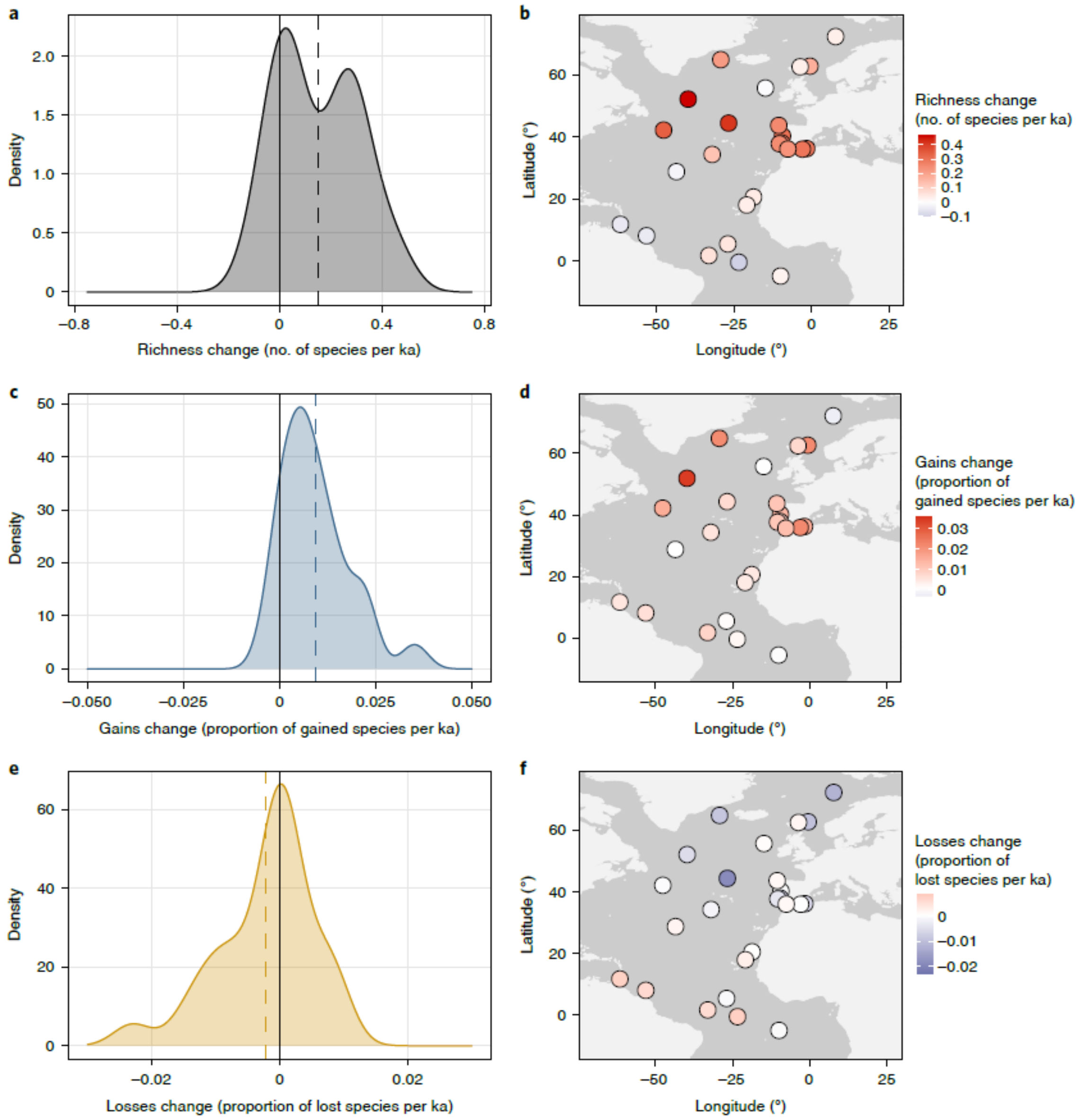

**Figure 3-3:** Local rates of biodiversity change of planktonic foraminifera in the past 24 kyr. **a–f**, Probability density functions and spatial distributions of rates of change in species richness (**a**,**b**) and the proportion of gained (**c**,**d**) and lost (**e**,**f**) species since the LGM. The rate of change is quantified for every time series as the slope of fitted linear models (see Methods and Extended Data Figures 3 and 4). Dashed vertical lines in the probability density functions indicate the overall mean in richness (**a**), gains (**c**) and losses (**e**)**,** and solid black lines indicate zero. Note the different scales of individual plots.

(Figure 3-3) led to the formation of new mid-latitude assemblages without analogues in the glacial ocean (Figure 3-4). With the beginning of the current warm period, these mid-latitude assemblages became compositionally even more dissimilar from assemblages that were present during the Last Glacial Maximum (LGM; 19-23 ka). Progressively, the composition of assemblages at higher (around 60°N) and lower (around 20°N) latitudes also departed from their nearest LGM analogues (Figure 3-4).

The asymmetry of local immigration and local extinction and the resulting transformation of the assemblage composition since the last ice age affected the development of the planktonic foraminifera LDG in the North Atlantic Ocean (Figure 3-5). The shape of the LDG continuously changed throughout the past 24 ka. The largest transformation of the LDG occurred between 30 and 50°N with an initial, transient decrease in species richness (Figure 3-5a) and Shannon diversity (Figure 3-5c) between 15 and 17 ka followed by a steady increase with highest values in the most recent time slices. At high latitudes, Shannon diversity and species richness remained stable over the transition from the last ice age to the current warm period but increased at around 11 ka with the increase being more prominent in diversity. Although the number of species in the tropics remained relatively stable during the past 24 ka (Figure 3-5b), Shannon diversity progressively declined (Figure 3-5d), leading to the flattening of the LDG in the tropics and ultimately the development of the present-day tropical diversity dip (Figure 3-5c).

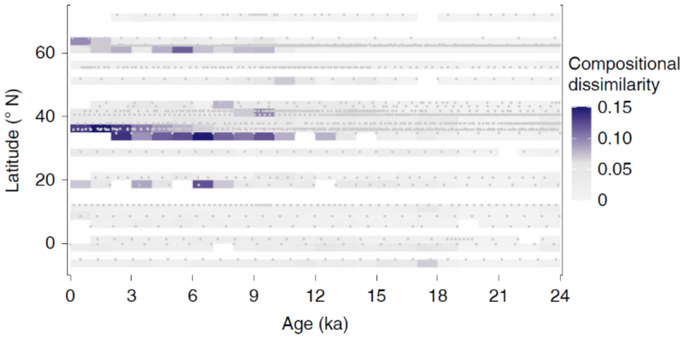

**Figure 3-4:** The emergence of no-analogue assemblages of planktonic foraminifera in the North Atlantic since the LGM. No-analogue assemblages are identified by compositional dissimilarity (Morisita-Horn distance) between a sample (grey dots) and the nearest LGM (19-23 ka) analogue higher than 0.06 (99th percentile of nearest-analogue distances within the LGM dataset; Extended Data Figure 5). Grid cells with values above and below the 0.06 threshold value are coloured in purple and grey, respectively. Grid cell resolution of the visualization: 1 kyr by 2.5° latitude.

## 3.3 Discussion

Even though the rate of global warming has markedly reduced with the beginning of the current warm period when compared to the last deglaciation, our observations indicate that planktonic foraminifera assemblages continued to change at the same pace as during the deglaciation after the transition to the current warm period ended (Figure 3-2a,c). This continuous transformation of assemblages during the current warm period lasted for at least 6 ka after the temperature forcing had stabilised (Figure 3-2), and could reflect the restructuring of ecological interactions, responses to other changing abiotic variables, and/or neutral drift (Hubbell, 2001; Liow et al., 2011). However, if neutral drift were the main control on turnover, one would expect assemblage change to not be in pace with climate change during the deglaciation and also to occur during the climatically stable period at the end of the last ice age prior to the onset of global warming (before 17 ka), which is not the case (Figure 3-2a). Alternatively, the continued assemblage change could reflect community restructuring due to asymmetric gains and losses during the warming-forced assemblage transformation (Figure 3-3). Prolonged phases of imbalance between local immigration and extinction have indeed been proposed for several species groups (Jackson and Sax, 2010; Hillebrand et al., 2018; Williams et al., 2021). This mechanism would imply that the timescale for reaching a new equilibrium in species turnover could be longer than the elapsed current warm period, indicating a very long (>10 ka) lag between temperature forcing and plankton response.

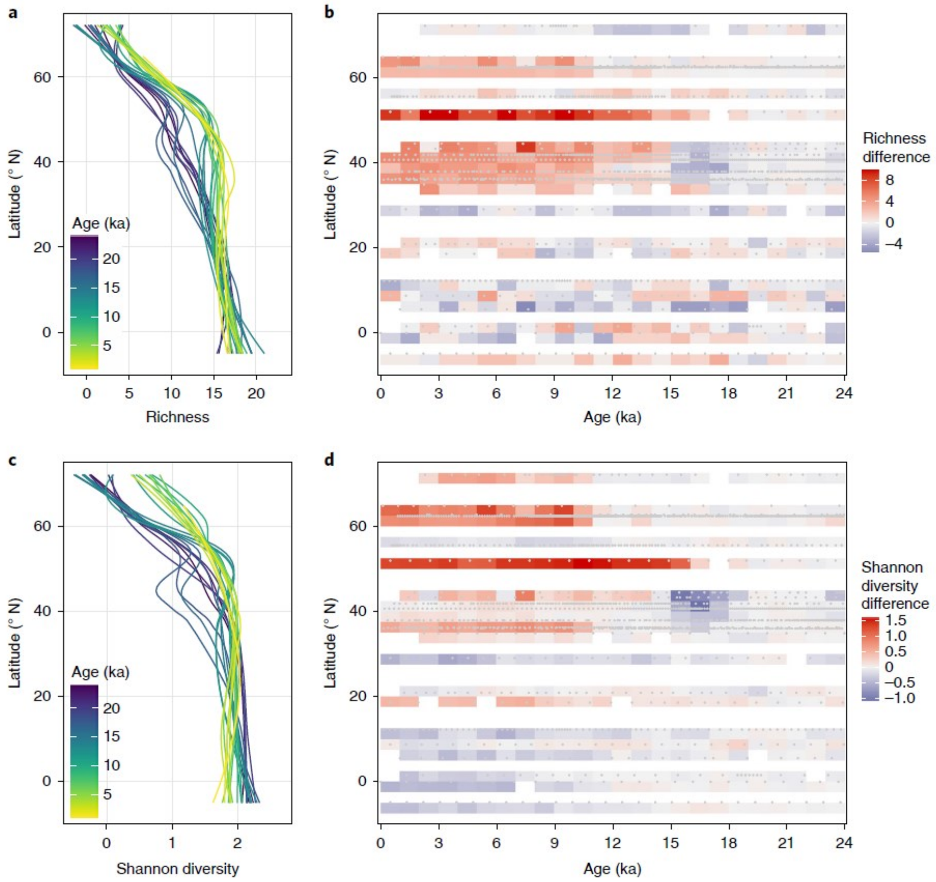

**Figure 3-5:** Evolution of the LDG in North Atlantic planktonic foraminifera for the past 24 kyr. **a,c**, LDGs based on species richness (**a**) and Shannon diversity (**c**) for the past 24 kyr expressed as locally fitted polynomial regression lines (LOESS fit) for all samples falling within one millennium. **b,d**, Differences in species richness (**b**) and Shannon diversity (**d**) from the LGM mean of each time series gridded at 1 kyr by 2.5° latitude. Grey dots represent individual samples.

Whilst assemblage turnover can take centuries to millennia to stabilise, as shown for many tree species and large mammals (Williams et al., 2021), our data show evidence against a lag in the response that is longer than the century-scale resolution of our time series. First of all, we observe no changes in the assemblage composition during the climatically stable period between 17 and 23 ka prior to the onset of global warming (Figure 3-2), even though this period was directly preceded by rapid and pronounced climate change before 27 ka (Van Meerbeeck et al., 2009). If there was a very long lag between forcing and plankton response, we would also expect to see an influence between 17 and 23 ka. Second, the local prevalence of subpolar-polar assemblages in the mid-latitudes between 15 and 17 ka (Figure 3-1b) documents a rapid response of the local fauna to the transient cooling and the subsequent warming caused by the Heinrich Event. It is possible that the direct response of planktonic foraminifera during the transition from the ice age (including the mid-latitude short-term cooling event) and the lagged and more complex response during the current warm period reflect faster response times of cold, species-poor assemblages compared to more species-rich warm-water assemblages. However, the most parsimonious explanation for the direct response would be that any lags in the assemblage response to climate change are shorter than the century-scale resolution of our time series and that the assemblage change during the current warm period does not reflect extinction debt (Jackson and Sax, 2010).

Thus, the question arises what could be the cause of the continued assemblage change. In this study, we use global mean surface temperature as a measure of climate change, but the assemblages responded to local rather than global mean forcing, as can be seen by the response to the mid-latitude short-term cooling event. In addition, global mean temperature is likely to be much less well correlated to local temperature during periods when the temperature changes are small. This might partly explain the discrepancy between global mean temperature and the overall planktonic foraminifera response in the current warm period, but it cannot explain the progressive emergence of novel assemblages. However, temperature might not be the only driver of plankton biogeography especially at lower latitudes8 and food availability has been shown to also be important for temporal dynamics of planktonic foraminifera species (Jonkers and Kučera, 2015; Ofstad et al., 2020). In addition, other environmental factors such as the amplitude of seasonal temperature change or the degree of stratification of the water column, which changed during the current warm period (Bova et al., 2021), might have contributed to the observed diversity patterns by the formation of new environmental vertical or seasonal niches.

Although it is difficult to decipher the exact cause of the continued change in the planktonic foraminifera assemblages during the current warm, stable period, one explanation could be a shift in the causes of species sorting in the planktonic foraminifera assemblages from abiotic-dominated causes (i.e. temperature forcing) during the last deglaciation to more biotic-dominated causes (e.g. changes in other plankton groups, food availability) during the current warm period. New direct and indirect ecological interactions between species of the same or other plankton groups might cause shifts in assemblage composition. Here we consider competition a less likely cause as Rillo et al. (2019) found no detectable evidence for interactions (i.e. interspecific competition) within the planktonic foraminifera group itself. Instead, the continued change in planktonic foraminifera assemblages could have occurred due to a reorganisation of their trophic interactions, reflecting changes in other aspects of the plankton community (e.g. changes in the timing and composition of seasonal blooms, changes in predation pressure or exposure to new pathogens).

Notwithstanding the exact cause, the community dynamics during the current warm period were essential for the development of the present-day biogeography of planktonic foraminifera, including the distinct LDG with a tropical diversity dip (Yasuhara et al., 2020b). We show that the flattening and ultimately the dip in tropical diversity in planktonic foraminifera evolved since the beginning of the current warm period at about 11 ka, at the end of the rapid deglacial warming (Figure 3-5). We also show that the present-day shape of the LDG (Figure 3-5a,c) is the result of species gains in the mid-latitudes (Figure 3-5b) combined with decreasing Shannon diversity in the tropics (Figure 3-5d). The decreasing Shannon diversity indicates that few species became more dominant leading to more uneven assemblages and suggests that the equatorial region became progressively less hospitable to some species that inhabited the tropics during the LGM during the current warm period. It is therefore indeed likely that further warming will lead to species losses in this region, resulting in a tropical diversity crisis as predicted by the macroecological model of Yasuhara et al. (2020b). We also show that assemblage transformations occurred across the entire latitudinal gradient. Thus, the exact future shape of the LDG remains unclear, because the continued warming could also lead to a loss of the surplus of species in the mid-latitudes resulting from the asymmetry of gains versus losses (Jackson and Sax, 2010).

The establishment of novel planktonic foraminifera assemblages during the current warm period (Figure 3-4) was the result of the poleward migration of species (Figure 3-1b) in combination with the asymmetry of local immigration and extinction (Figure 3-3). These asymmetrical shifts in species ranges induced by warming have also been observed and modelled in other marine taxa (Poloczanska et al., 2013; García Molinos et al., 2016; Antão et al., 2020). However, we show that the postglacial surplus of species in the mid-latitudes (Figure 3-3) was not lost by delayed local extinctions in these regions (extinction debt payment; Jackson and Sax, 2010) and that these novel assemblages are not a transient phenomenon of species response to global warming. Instead, we show that the compositional uniqueness of these assemblages persists for millennia after the rapid deglacial warming. This provides observational constraints for modelling, indicating that the projected future warming could also lead to the assembly of long-lasting novel marine communities (García Molinos et al., 2016; Antão et al., 2020) with potentially important consequences for key ecosystem functions.

## 3.4 Methods

### 3.4.1 Data

The community change analyses are based on 25 planktonic foraminifera assemblage time series covering the past 24 ka with an average resolution of 0.60 ka, ranging from 0.04 to 1.31 ka (Extended Data Table 3-1). Throughout this contribution, age information is provided in calibrated radiocarbon years, so 0 ka is 1950 Common Era. The series were selected from among 198 records situated in the North Atlantic Ocean and adjacent seas initially identified in public databases as containing planktonic foraminifera assemblage counts spanning the transition from the last ice age to the current warm period. Of these, only time series where the entire assemblages have been counted were used and further limited to time series that record the entire time period of interest, i.e. beginning at least at 23 ka and ranging to at least 3 ka with a resolution below 1.5 ka to resolve millennial-scale climate events. The remaining 25 time series cover the full latitudinal and thermal gradient in the North Atlantic Ocean (Figure 3-1a). For the 9 sites included in the PALMOD 130k marine palaeoclimate data synthesis V1.1 (Jonkers et al., 2020), we used their provided revised age models based on radiocarbon ages and benthic foraminifera oxygen isotope data which were manually tuned to regional benthic foraminifera oxygen isotope stacks (Lisiecki and Stern, 2016). Their radiocarbon ages were re-calibrated using the IntCal13 calibration curve (Reimer et al., 2013) using reservoir ages based on a comprehensive ocean general circulation model (Butzin et al., 2017). For the 16 sites not included in the PALMOD 130k marine palaeoclimate data synthesis V1.1 (Jonkers et al., 2020), the same approach as in Jonkers et al. (2020) was used to revise the published age models to ensure the comparability of all analysed sites (Extended Data Table 3-1). The age model revisions were conducted with PaleoDataView (Langner and Mulitza, 2019).

Assemblage composition of planktonic foraminifera in the LGM ocean was analysed using a regional North Atlantic subset of the MARGO compilation (Kucera et al., 2005a). Covering the same latitudinal range as the 25 time series used in this study (i.e., 90°N to 6°S). Samples from the time series of this study that belonged to the LGM interval but were not present in the MARGO synthesis (i.e. published after 2005) were also added to the LGM dataset (194 samples from 14 sites). We used the LGM time interval as defined by Mix et al. (2001) and in the MARGO compilation (Kucera et al., 2005a) of 19-23 ka. In total, the updated LGM compilation consists of 1083 assemblage compositions from 173 unique sites (Extended Data Figure 3-2). The global mean surface temperature (Figure 3-2c) used for the comparison with the overall response of the planktonic foraminifera assemblages is the result of a data assimilation approach that combines 539 proxy records with independent model information (Osman et al., 2021). The temperature anomalies are referenced to the mean of the past two millennia (0-2 ka).

All planktonic foraminifera assemblage count data used here were harmonised taxonomically following Siccha and Kucera (2017). Species not reported in the time series data were assumed to be absent (i.e., zero abundance). We merged *Globigerinoides ruber ruber* and *Globigerinoides ruber albus*, because some studies only reported them together as *Globigerinoides ruber*. Also, P/D intergrades (an informal category of morphological intermediates between *Neogloboquadrina incompta* and *Neogloboquadrina dutertrei*) were merged with *Neogloboquadrina incompta*. In total, 41 species of planktonic foraminifera were included in our study (Extended Data Table 3-2).

### 3.4.2 Spatio-temporal compositional dissimilarity

To visualise which time periods and regions in the oceans have similar species composition (Figure 3-1b), we calculated the compositional dissimilarity between all pairwise combinations of all samples in the 25 time series (1840 samples in total). The compositional dissimilarity was calculated using the Morisita-Horn (M-H) index (Horn, 1966):

$$C = 1 - \frac{2 \cdot \sum_{i=1}^{S}(x_i \cdot y_i)}{\sum_{i=1}^{S} x_i^2 + \sum_{i=1}^{S} y_i^2}$$

with $S$ being the total number of species in both samples and $x_i$ and $y_i$ being the relative abundances of the $i$-th species in both samples. The M-H index is a turnover measure based on distance that is relatively independent of sample size and robust to under-sampling (Jost et al., 2011). The measure ranges from 0 to 1 with 0 meaning an identical composition of the two samples and 1 indicating no shared species. We then applied a Principal Component Analysis (PCA) to the compositional dissimilarity matrix to reduce its dimensionality and visualise the spatio-temporal evolution of assemblage composition. The first three PC axes explained more than 97% of the variance and we assigned a RGB value to each of these axes (PC1 blue, PC2 red, PC3 green; Ferrier et al., 2007). As a result, each sample of our study had an RGB value related to its projection in the PC dissimilarity space. These RGB values were then plotted in a Hovmoller-like plot (Figure 3-1b) where similar colours in the grid correspond to similar species compositions.

### 3.4.3 PCA on species composition

To determine the temporal pattern of compositional change in the analysed planktonic foraminifera time series, we applied a PCA for each time series on the species assemblage data and extracted for each time series the axis that explains most variance in the assemblage data (PC1). We fitted linear models through all PC1 axes to check and, if necessary, change the polarisation to align all PC1 axes in the same direction. To adjust for different resolutions of the individual records, we interpolated the PC1 scores at 0.5 ka bins and restricted the interpolated data to the interval that is covered by all time series (2.5-23 ka), to prevent edge effects. Because the shape of the faunal trends at all sites was similar, we visualised the overall trend of faunal response among the 25 time series by a polynomial regression using a locally estimated scatterplot smoothing (LOESS, using standard settings) on the interpolated individual PC1 axes scores (Figure 3-2a).

### 3.4.4 Species gains and losses

To analyse local biodiversity change, we first calculated species richness (Figure 3-3a,b) at every location and time step and the proportion of species gained (Figure 3-3c,d) and lost (Figure 3-3e,f) compared to the LGM (oldest sample in the time series). Species gains and losses 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 that time series relative to the total number of species observed in both samples pooled together, taking species identity into account (Antão et al., 2020; see Extended Data Figure 3-3). We then calculated the slopes of fitted linear models for species richness, gains and losses to quantify the rates of biodiversity change (see Extended Data Figure 3-4). The rate of richness change is given in species per unit time and the rates of gains and losses change are given in the proportion of gained or lost species (compared to the oldest sample in the time series) per unit time over the entire length of the time series. A positive slope in richness indicates an increase in the number of species through time and a negative slope means a decrease. For gains (losses), a positive slope indicates that the proportion of species gained (lost) at a given site compared to the oldest sample in the time series increases through time, meaning species gains (losses) are accumulated through time leading to an increase (decrease) of species richness. Time series where the proportion of gained (lost) species is decreasing through time show a negative slope.

### 3.4.5 No-analogues assemblages

To investigate the potential formation of new assemblages during the planktonic foraminifera response to deglacial warming after the LGM, we calculated for each assemblage in the time series the compositional dissimilarity (M-H index) to all the assemblages from the LGM compilation (see data section). We then obtain the distance to the nearest analogue from the minimum dissimilarity. Figure 3-4 shows these minima gridded in a Hovmoller-like plot. To judge whether or not the observed minimum M-H distance indicated a no-analogue assemblage, we calculated M-H-index values for each of the LGM compilation samples relative to the remaining samples in the compilation, thus obtaining threshold values for M-H index dissimilarities that do not necessarily represent no-analogue faunas and could occur by chance. We calculated the 95 and 99 percentiles of the M-H distances to the nearest (as well as 2nd- and 3rd-nearest) non-self analogue within the LGM compilation (Extended Data Figure 3-2) and compared it with the observed no-analogue values. We find that 99 % of the LGM samples have a nearest analogue with a dissimilarity of less than 0.06 (as well as 2nd-nearest analogue of <0.09 and 3rd-nearest analogue of <0.11) within the LGM dataset (Extended Data Figure 3-5). Therefore, we claim that the dissimilarities of 0.15-0.25 that we observe in the mid-latitudes in the Holocene samples (Figure 3-4) are significantly higher than what we could expect to happen by chance, pointing to changing assemblages with no LGM analogue.

### 3.4.6 LDG through time

To visualise the temporal evolution of the planktonic foraminifera LDG in the North Atlantic Ocean, we pooled all samples from each time series together within millennial bins and calculated the number of species (richness) and the Shannon entropy (Shannon, 1948), an abundance-based diversity metric:

$$H_S = -\sum_{i=1}^{S} p_i \cdot \log p_i$$

with $S$ being the number of species at a specific site and $p_i$ being the relative abundance of the $i$-th species. Because relative abundances are always between 0 and 1, the higher the metric, the more diverse the assemblage. The latitudinal gradients of species richness and Shannon diversity were then visualised for each millennium by polynomial regressions using a locally estimated scatterplot smoothing (LOESS) (Figure 3-5a,c).

To understand when and where diversity change occurred during the past 24 ka, we calculated for each sample, the difference between its richness and Shannon diversity and the mean LGM richness and Shannon diversity of the site. The mean LGM richness and Shannon diversity were calculated across all samples in a given time series that fall within 19-23 ka. These differences were then gridded in Hovmoller-like plots with a grid cell resolution in time and space of 1 ka and 2.5° (Figure 3-5b,d).

### 3.4.7 R packages

All statistical analyses were performed with R version 4.1.3 (R Core Team, 2024) using the tidyverse (Wickham et al., 2019) and the janitor (Firke, 2023) packages for cleaning and importing the data; vegan (Oksanen et al., 2020) and codyn (Hallett et al., 2016) for beta diversity and community structure analyses; rioja (Juggins, 2020) for the nearest analogue analysis; FactoMineR (Lê et al., 2008) for the PCA analysis; and ggplot2 (Wickham, 2016), raster (Hijmans, 2023) and vidiris (Garnier, 2021) for the plots.

## Data availability

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 Extended Data Table 1.

MARGO data that are used for the regional North Atlantic LGM dataset are available on PANGAEA (Atlantic Ocean: https://doi.pangaea.de/10.1594/PANGAEA.227329, Mediterranean: https://doi.pangaea.de/10.1594/PANGAEA.227306 and Pacific: https://doi.pangaea.de/10.1594/PANGAEA.227327). 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/). Taxonomically harmonized assemblage data are available at https://doi.org/10.5281/zenodo.6948750.

## Code availability

R code used to generate the results of this study are available at https://doi.org/10.5281/zenodo.6948750.

## Acknowledgements

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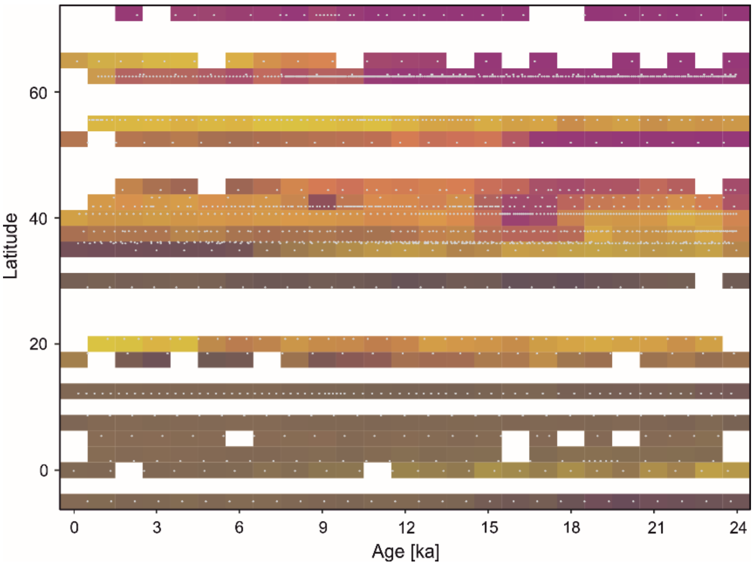
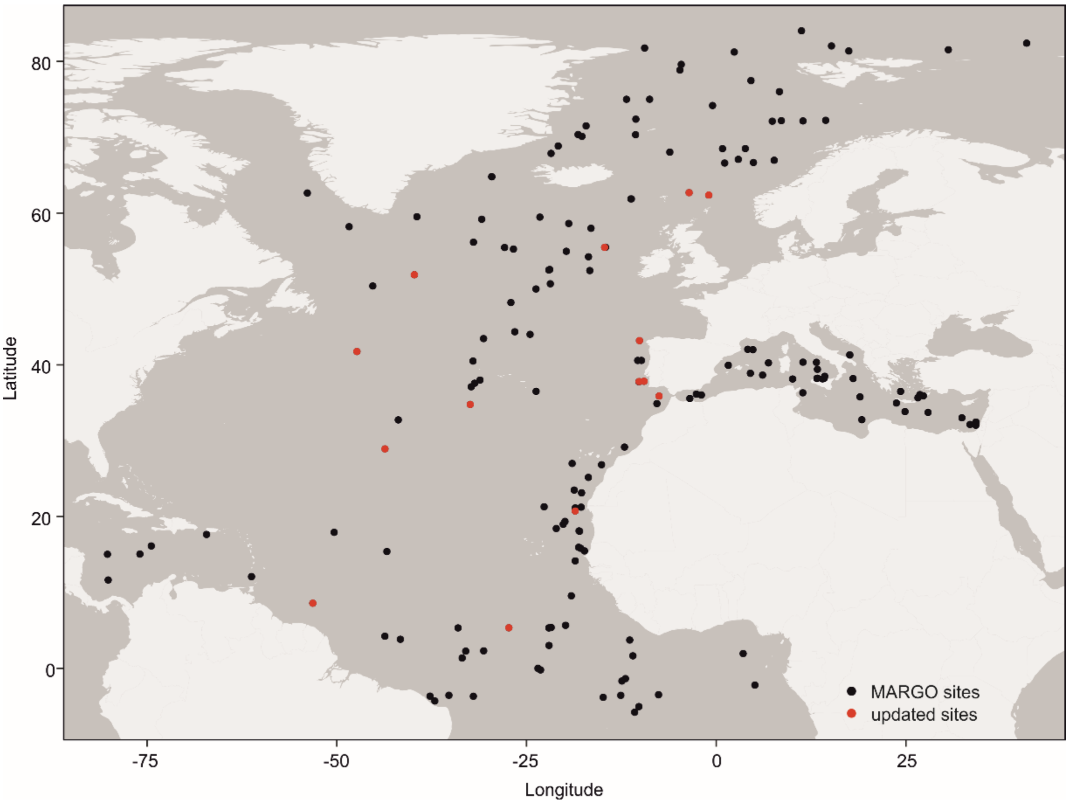
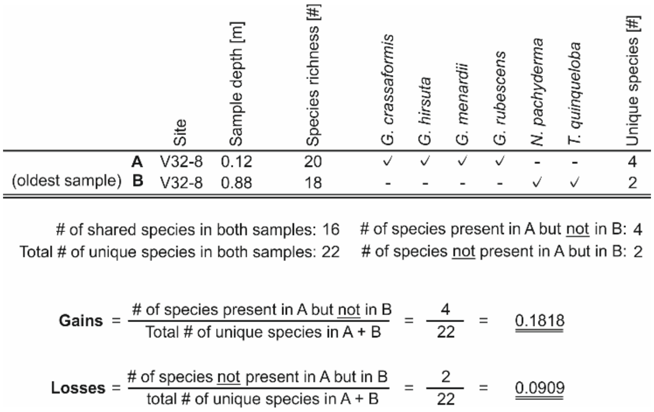
## 3.5 Extended data



**Extended Data Figure 3-1:** Colour-blind friendly visualisation of the spatiotemporal pattern of the overall assemblage change. This figure shows the colour-blind friendly version of Figure 3-1b for each analysed assemblage (grey dots), gridded at 1 ka by 2.5° latitude. We again use the first three PCs that explain more than 97 % of the variance in the compositional dissimilarity matrix (see method section), but instead of assigning RGB values to the PC scores, we here mix different colour palettes for each PC using individual colours from the plasma colour palette. One colour palette was calculated for PC1 (from yellow to purple) and another one for PC2 (from orange to dark blue). These palettes were then mixed with the ratio defined by PC3. Similar colours in the grid correspond to similar species compositions.



**Extended Data Figure 3-2:** Overview map of LGM dataset. Updated LGM compilation (1083 samples from 173 sites) used to assess the LGM assemblage analogues. This compilation is based on a MARGO subset (Kucera et al., 2005a) that was updated with samples from the time series used in this study that belonged to the LGM interval (194 samples from 14 sites). The geographical extent was restricted to the North Atlantic Ocean (including the Mediterranean Sea and the Arctic Ocean) and the same latitudinal extent as the 25 time series used in this study (that is, up to a latitude of 6°S).



| | | Site | Sample depth [m] | Species richness [#] | *G. crassaformis* | *G. hirsuta* | *G. menardii* | *G. rubescens* | *N. pachyderma* | *T. quinqueloba* | Unique species [#] |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | **A** | V32-8 | 0.12 | 20 | ✓ | ✓ | ✓ | ✓ | - | - | 4 |
| (oldest sample) | **B** | V32-8 | 0.88 | 18 | - | - | - | - | ✓ | ✓ | 2 |

# of shared species in both samples: 16

Total # of unique species in both samples: 22

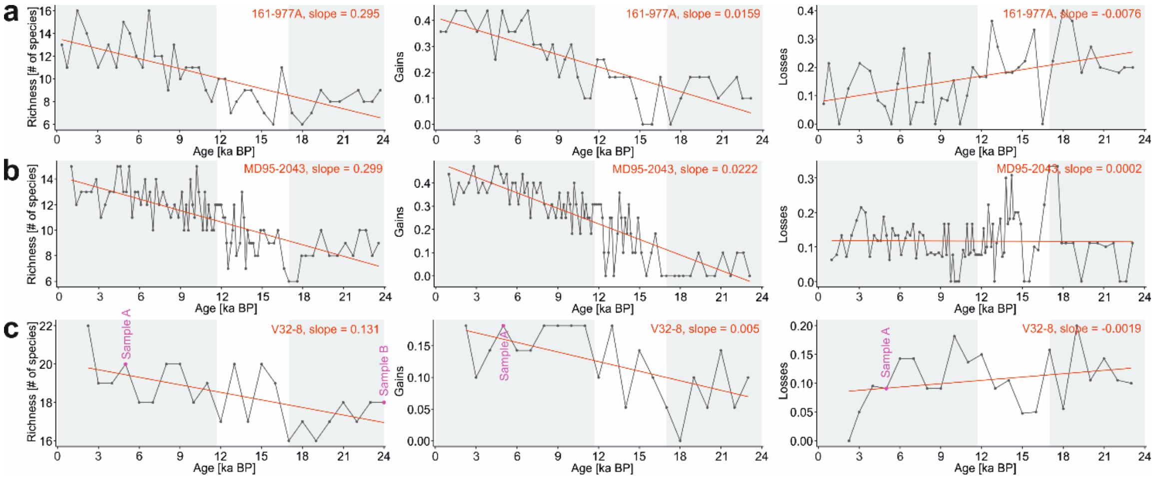
# of species present in A but not in B: 4

# of species not present in A but in B: 2

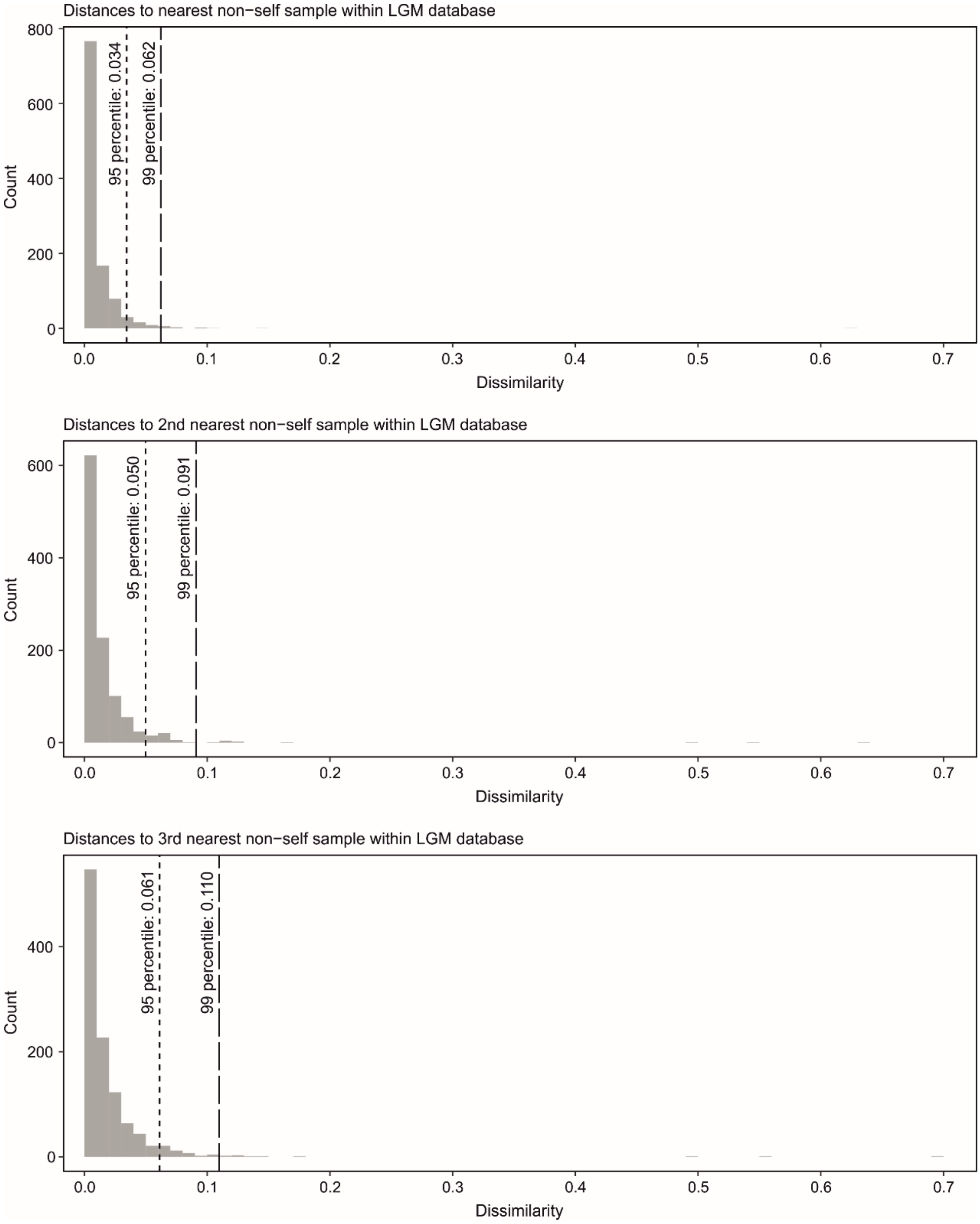
$$\textbf{Gains} = \frac{\text{\# of species present in A but } \underline{\text{not}} \text{ in B}}{\text{Total \# of unique species in A + B}} = \frac{4}{22} = \underline{\underline{0.1818}}$$

$$\textbf{Losses} = \frac{\text{\# of species } \underline{\text{not}} \text{ present in A but in B}}{\text{total \# of unique species in A + B}} = \frac{2}{22} = \underline{\underline{0.0909}}$$

**Extended Data Figure 3-3:** Example for gains and losses calculation. This example shows the calculation of the gains and losses values for Sample A (site V32-8; 0.12 m depth). For the gains and losses calculation, all samples in a time series are always compared to the oldest sample in that time series (here Sample B; site V32-8; 0.88 m depth). Sample A contains 20 species with 4 (G. crassaformis, G. hirsuta, G. menardii and G. rubescens) not being present in Sample B, whereas Sample B (18 species) contains 2 species (N. pachyderma and T. quinqueloba) not present in sample A. Both samples share 16 species. Gains are calculated as the proportion of the number of species present in Sample A but not in Sample B relative to the total number of species in both samples pooled together (22 species: 16 shared plus 6 unique species) resulting in a gain value of 0.1818. Losses are calculated as the number of species not present in Sample A but present in Sample B relative to the total number of species in both samples resulting in a loss value of 0.0909. Sample A and B are also highlighted in Extended Data Figure 3-4c.



**Extended Data Figure 3-4:** Example of fitted linear models. To quantify the rates of biodiversity change we calculated the slope of fitted linear models for species richness, gains and losses. Here, the fitted linear models are shown for three exemplary sites: 161-977A (**a**), MD95-2043 (**b**) and V32-8 (**c**). Species richness is the absolute number of species in each sample. A positive slope in richness indicates an increase in the number of species since the LGM and a negative slope means a decrease. Gains and losses are given as the proportion between the gained/lost species in each sample compared to the oldest sample in each time series relative to the total number of species in both samples pooled together (see Extended Data Figure 3-3); since gains and losses are given as proportions, they are unitless. For gains (losses), a positive slope indicates that the number of species gained (lost) at a given site increased over time. Time series in which the number of gained (lost) species is decreasing through time show a negative slope. In other words, a positive slope of species gains (losses) means that the richness is increasing (decreasing) continuously through time as species gains (losses) are accumulating through time. A slope of species gains/losses equals zero means that the richness remains constant over time as no species gains are accumulated through time. Red lines correspond to the fitted linear models and the slopes are given in the upper right corner of each panel. **c**, also shows the temporal location of Sample A and B used in Extended Data Figure 3-3.



**Extended Data Figure 3-5:** Histogram of nearest non-self analogues. Distance to nearest (as well as 2nd and 3rd nearest) non-self analogue within LGM compilation (see Extended Data Figure 3-2). 99 % of the LGM samples have a nearest analogue with a dissimilarity of less than 0.06.

### Extended Data Table 3-1: Overview of time series

| | Latitude | Longitude | Depth | Resolution | Assemblage data | | Metadata used for age models | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| **Core** | **north [°]** | **east [°]** | **[m]** | **[ka]** | **Reference** | **Data** | **14C ref.** | **14C data** | **Iso ref.** | **Iso data** |
| **GIK17730-4** | 72.11 | 7.39 | -2749 | 0.63 | (Schulz, 1995a) | (Schulz, 1995b) | (Sarnthein et al., 1995) | (Sarnthein, 2003) | - | - |
| **V28-14** | 64.78 | -29.57 | -1855 | 1.31 | (CLIMAP Project Members, 1981) | (CLIMAP Project Members, 2009) | * | | | |
| **MD99-2285** | 62.69 | -3.57 | -885 | 0.58 | (Wary et al., 2017) | ** | (Wary et al., 2017) | ** | - | - |
| **MD99-2284** | 62.37 | -0.98 | -1500 | 0.04 | (Eldevik et al., 2014) | (Dokken et al., 2015) | (Rasmussen et al., 2006; Svensson et al., 2008; Bakke et al., 2009; Risebrobakken et al., 2011; Dokken et al., 2013) | ** | - | - |
| **162-980** | 55.48 | -14.70 | -2180 | 0.23 | (Benway et al., 2010) | (Benway et al., 2013) | * | | | |
| **SU90-I03** | 51.88 | -39.78 | -2970 | 0.96 | (Schulz, 1995a) | (Schulz, 1995c) | - | - | (Schulz, 1995a) | (Schulz, 1995d) |
| **GIK15612-2** | 44.36 | -26.54 | -3050 | 0.63 | (Kiefer, 1998) | (Kiefer and Sarnthein, 1998) | * | | | |
| **SU92-03** | 43.20 | -10.11 | -3005 | 0.67 | (Salgueiro et al., 2010b) | (Salgueiro et al., 2010a) | (Salgueiro et al., 2010b) | ** | (Salgueiro et al., 2010b) | (Salgueiro et al., 2010c) |
| **CH69-K09** | 41.76 | -47.35 | -4100 | 0.18 | (Labeyrie et al., 1999) | (Labeyrie et al., 2017) | * | | | |
| **MD95-2040** | 40.58 | -9.86 | -2465 | 0.15 | (de Abreu et al., 2003a) | (de Abreu et al., 2003b) | * | | | |
| **MD95-2041** | 37.83 | -9.51 | -1123 | 0.34 | (Voelker and de Abreu, 2011b) | (Voelker and de Abreu, 2011a) | (Voelker and de Abreu, 2011b) | (Voelker and de Abreu, 2011c) | (Voelker et al., 2009a) | (Voelker et al., 2009b) |
| **MD95-2042** | 37.80 | -10.17 | -3146 | 0.27 | (Chabaud et al., 2014) | (Rossignol, 2022) | (Chabaud et al., 2014) | ** | (Cayre et al., 1999a) | (Cayre et al., 1999b) |
| **MD95-2043** | 36.14 | -2.62 | -1841 | 0.26 | (Pérez-Folgado et al., 2003e) | (Pérez-Folgado et al., 2003b) | * | | | |
| **161-977A** | 36.03 | -1.96 | -1984 | 0.56 | (Pérez-Folgado et al., 2003e) | (Pérez-Folgado et al., 2003a) | (Pérez-Folgado et al., 2003e) | (Pérez-Folgado et al., 2003d) | (Pérez-Folgado et al., 2003e) | (Pérez-Folgado et al., 2003c) |
| **MD99-2339** | 35.89 | -7.53 | -1177 | 0.19 | (Eynaud et al., 2009; Voelker and de Abreu, 2011b) | (Voelker et al., 2010) | * | | | |
| **V32-8** | 34.78 | -32.42 | -3252 | 0.95 | (Mix, 1986) | (Mix, 2006e) | - | - | (Mix, 1986) | (Mix, 1999a) |
| **V22-222** | 28.93 | -43.65 | -3197 | 0.83 | (Mix, 1986) | (Mix, 2006a) | - | - | (Mix et al., 1986a) | (Mix et al., 1986b) |
| **108-658C** | 20.75 | -18.58 | -2273 | 0.59 | (Haslett and Smart, 2006) | - | (deMenocal et al., 2000a) | (deMenocal et al., 2000b) | - | (Knaack and Sarnthein, 2005) |
| **V30-49** | 18.43 | -21.08 | -3093 | 1.02 | (Mix, 1986) | (Mix, 2006d) | (Mix and Ruddiman, 1985) | (CLIMAP Project Members, 2004d) | (Mix, 1986; McIntyre et al., 1989) | (Ruddiman, 1997; Mix, 2003c) |
| **M35003-4** | 12.09 | -61.24 | -1299 | 0.31 | (Hüls, 2000) | (Hüls, 1999) | * | | | |
| **V25-75** | 8.58 | -53.17 | -2743 | 0.81 | (Mix, 1986) | (Mix, 2006c) | (Mix and Ruddiman, 1985) | (CLIMAP Project Members, 2004a) | (Mix, 1986) | (Mix, 1999b, 2003a) |
| **V30-36** | 5.35 | -27.32 | -4245 | 1.02 | (Mix et al., 1999d) | (Mix et al., 1999b) | (Mix and Ruddiman, 1985) | (CLIMAP Project Members, 2004b) | (Mix, 1986) | (Mix, 2003b) |
| **V25-59** | 1.37 | -33.48 | -3824 | 0.75 | (Mix, 1986) | (Mix, 2006b) | * | | | |
| **V30-40** | -0.20 | -23.15 | -3706 | 0.99 | (Mix et al., 1999d) | (Mix et al., 1999c) | (Mix and Ruddiman, 1985) | (CLIMAP Project Members, 2004c) | (McIntyre et al., 1989) | (McIntyre and Imbrie, 2000) |
| **RC24-16** | -5.04 | -10.19 | -3543 | 0.83 | (Mix et al., 1999d) | (Mix et al., 1999a) | - | - | (McIntyre et al., 1989) | (Imbrie and McIntyre, 2000) |

*age model from PALMOD 130k marine palaeoclimate data synthesis V1.1(Jonkers et al., 2020) was used

**from paper/s or online supplements

**Extended Data Table 3-2:** Species list of planktonic foraminifera

| # | Species name | # | Species name |
|---|---|---|---|
| 1 | *Beella digitata* | 21 | *Globorotalia menardii* |
| 2 | *Berggrenia pumilio* | 22 | *Globorotalia scitula* |
| 3 | *Candeina nitida* | 23 | *Globorotalia theyeri* |
| 4 | *Dentigloborotalia anfracta* | 24 | *Globorotalia truncatulinoides* |
| 5 | *Globigerina bulloides* | 25 | *Globorotalia tumida* |
| 6 | *Globigerina falconensis* | 26 | *Globorotalia ungulata* |
| 7 | *Globigerinella adamsi* | 27 | *Globorotaloides hexagonus* |
| 8 | *Globigerinella calida* | 28 | *Globoturborotalita rubescens* |
| 9 | *Globigerinella siphonifera* | 29 | *Hastigerina pelagica* |
| 10 | *Globigerinita glutinata* | 30 | *Hastigerinella digitata* |
| 11 | *Globigerinita minuta* | 31 | *Neogloboquadrina dutertrei* |
| 12 | *Globigerinita uvula* | 32 | *Neogloboquadrina incompta* |
| 13 | *Globigerinoides conglobatus* | 33 | *Neogloboquadrina pachyderma* |
| 14 | *Globigerinoides ruber* | 34 | *Orbulina universa* |
| 15 | *Globigerinoides tenellus* | 35 | *Pulleniatina obliquiloculata* |
| 16 | *Globoconella inflata* | 36 | *Sphaeroidinella dehiscens* |
| 17 | *Globoquadrina conglomerata* | 37 | *Tenuitella iota* |
| 18 | *Globorotalia cavernula* | 38 | *Tenuitella parkerae* |
| 19 | *Globorotalia crassaformis* | 39 | *Trilobatus sacculifer* |
| 20 | *Globorotalia hirsuta* | 40 | *Turborotalita humilis* |
|  |  | 41 | *Turborotalita quinqueloba* |

# 4 Manuscript II

## Coherent response of zoo- and phytoplankton assemblages to global warming since the last ice age

**T. Strack, L. Jonkers, M.C. Rillo, K.-H. Baumann, H. Hillebrand, and M. Kucera**

Submitted to *Global Ecology and Biogeography* in 2023

**Addendum 17/04/2024**: A revised version of this manuscript has been accepted for publication in *Global Ecology and Biogeography* on 21 March 2024 and is available at DOI: 101111/geb.13841. This revised version includes coccolithophore assemblage data from two additional sites, which alters the overall coccolithophore pattern presented here in this draft.

### Structured Abstract

**Aim:** We use the fossil record of different marine plankton groups to determine how their biodiversity responded to past climatic change with a magnitude comparable to projected future warming.

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

**Time period:** Past 24,000 years, i.e., from the last cold stage to the current warm period covering the last deglaciation.

**Major taxa studied:** Planktonic foraminifera, dinoflagellates and coccolithophores.

Methods: We explore spatio-temporal patterns of biodiversity change across the last deglaciation. For this we use principal component analysis and generalised additive models to estimate the overall trend of temporal compositional change in each plankton group and identify time 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 Last Glacial Maximum mean.

**Results:** All three groups show comparable patterns of biodiversity change and overall assemblage change through time. In general, assemblages started to change with the onset of global warming around 16,000 to 17,000 years ago and continued to change at the same pace during the current warm period until at least 4,000 to 5,000 years ago.

**Main conclusions:** The climate change during the transition from the last cold stage to the current warm period led to a long-lasting reshuffling of the zoo- and phytoplankton assemblages likely associated with 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. These findings indicate that future global warming might also have long-term consequences for marine plankton communities.

## 4.1 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 the biodiversity dynamics we observe in nature may be caused by different processes, such as ecological drift, natural selection, or dispersal (as well as speciation on longer time scales) and these processes might interact in numerous ways (Vellend, 2010). On shorter time scales, 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 have been shown for different marine plankton species (Lohbeck et al., 2012; Geerts et al., 2015; Padfield et al., 2016; Bach et al., 2018). Also, geographical range shifts have been observed in many species across different environments (for reviews, see Walther et al., 2002; Root et al., 2003; Parmesan, 2006; Poloczanska et al., 2013) and are especially common in marine plankton groups, because of their high potential for dispersal due to ocean currents and the lack of physical barriers in the marine realm (Poloczanska et al., 2013; Lenoir et al., 2020). Considering the complexity of the marine realm and the multi-layered 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. This phenomenon is for example manifested as the observed asymmetry between the leading and trailing edges of species range shift provides evidence for expanding species interacting with persistent ones forming novel assemblages (Chen et al., 2011b; Poloczanska et al., 2013; García Molinos et al., 2016; Antão et al., 2020).

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, they rarely span more than 100 years (Dornelas et al., 2018), resulting in small observed environmental change compared to the expected magnitude of future global change. The fossil record can expand this observational window and, indeed, 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 global warming (Morey et al., 2005; Yasuhara et al., 2020b; Rillo et al., 2021). Even though the marine plankton consist mainly of soft-bodied organisms that have no fossilisation potential (Buitenhuis et al., 2013), several plankton groups secrete resistant organic or inorganic skeletons 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 and Kidwell, 2009; Yasuhara et al., 2012a). Many marine plankton groups that are preserved in the sediment record have been shown to be sensitive to ongoing climate change (coccolithophores: Rost and 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 (e.g., de Vernal et al., 2005; Gersonde et al., 2005; Kucera et al., 2005a; Kucera et al., 2005b). However, their potential to reveal biodiversity changes across continuous time periods of environmental change has been less explored.

Recently, Strack et al. (2022) used the fossil record of planktonic foraminifera to study their response 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 ice age to the current warm period (i.e., the Holocene). Planktonic foraminifera assemblages started to change immediately with the onset of global warming, but their shift continued during the current warm period, when climate change was not that prevalent anymore (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 on planktonic foraminifera only, however, it is important to investigate how general these results are; in other words, whether these observed biodiversity dynamics during the last deglaciation also happened in other plankton groups, especially among the phytoplankton, which is characterised by higher species richness, shorter generation times and potentially other environmental drivers.

To assess how other groups of plankton next to planktonic foraminifera responded to climate change during the last deglaciation, we here also study the response of fossil coccolithophores and dinoflagellates. Planktonic foraminifera are calcifying zooplankton that are either heterotrophic through predation and grazing or mixotrophic as some species bear unicellular algae as endosymbionts (Schiebel and Hemleben, 2017; Takagi et al., 2019). There are approximately 50 extant morphospecies (Brummer and Kučera, 2022) and their distribution and diversity are mainly correlated with sea surface temperature (Morey et al., 2005; Rillo et al., 2021). Coccolithophores are calcifying phytoplankton that are mainly autotrophic. There are about 280 known extant coccolithophore species, of which about 120 produce species-specific fossils that are preserved in sediments (Young et al., 2005). The main predictor of coccolithophore distribution is sea surface temperature and light availability (Mohan et al., 2008; Charalampopoulou et al., 2016; O'Brien et al., 2016). Dinoflagellates are a mixotrophic group, with some taxa being mainly autotrophic and other taxa exclusively heterotrophic (Stoecker, 1999; Jeong et al., 2005; Taylor et al., 2008). There are approximately 2,000 known extant dinoflagellate species (Taylor et al., 2008). Living dinoflagellates are not fossilisable, but about 13% to 16% of dinoflagellate species produce organic-walled resting cysts which are preserved in the sediment (Head, 1996). The biogeography of dinoflagellates is mainly predicted by temperature, but other factors such as productivity and nutrient availability also play a role (Esper and Zonneveld, 2002; Taylor et al., 2008; Chen et al., 2011a; Hohmann et al., 2020). By also considering coccolithophores and dinoflagellates, our study design includes plankton groups that differ in their diversity, trophic strategy and preservation. Also, the groups differ in terms of their ecological importance and functions. Planktonic foraminifera and coccolithophores are two main contributors to the pelagic carbonate flux (Schiebel, 2002; Rost and Riebesell, 2004), whereas coccolithophores and dinoflagellates are primary producers, playing an important role in the organic carbon flux (Rost and Riebesell, 2004; Bravo and Figueroa, 2014). All three plankton groups show a strong latitudinal diversity gradient in the North Atlantic Ocean with lowest diversities at the highest latitudes and a peak in diversity in the sub-tropics rather than the tropics (Rutherford et al., 1999; Boeckel and Baumann, 2008; Tittensor et al., 2010; Chen et al., 2011a; Fenton et al., 2016b; O'Brien et al., 2016; Yasuhara et al., 2020b).

Using time series of assemblage (sensu Fauth et al., 1996) composition data since the last ice age, we examine how planktonic foraminifera, coccolithophores and dinoflagellates responded to the environmental forcing during the last deglaciation - a climatic upheaval that is comparable to projected future global warming (Jackson and Overpeck, 2000). If the main predictor of the biogeography of these three plankton groups was temperature 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 common forcing could differ. This would also be the case, if evolutionary response and adaptation in any of the groups would be faster, as has been hypothesised for coccolithophores (Beaufort et al., 2022; Bendif et al., 2023).

## 4.2 Methods

### 4.2.1 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 4 coccolithophore and 6 organic-walled dinoflagellate cyst (dinocyst) assemblage time series to compare the patterns across groups (see Extended Data Table 4-1). 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 of the entire assemblages (i.e., all individuals identified and counted), are located in the North Atlantic Ocean and adjacent seas, span the time period from the last ice age to the current warm period (i.e., past 24 kyr, but at least from 22.5 ka to 3.5 ka), and have enough 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; Zonneveld et al., 2008; Zonneveld et al., 2019). However, we assume aerobic degradation to not be 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 dinocysts time series (see also Holzwarth et al., 2010a).

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.

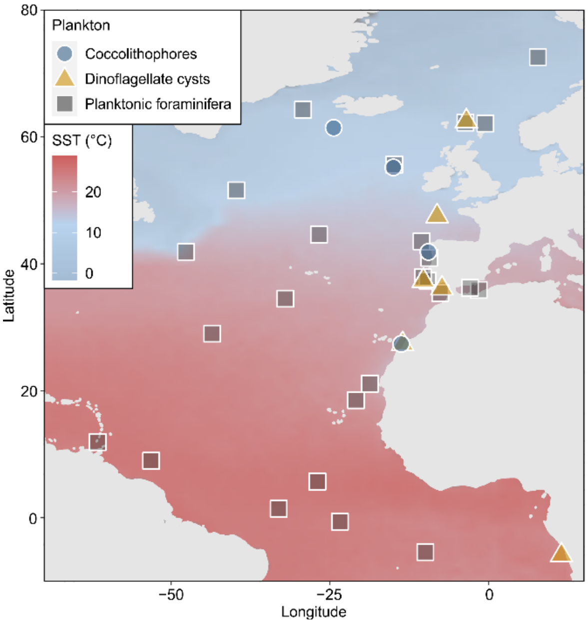


**Figure 4-1:** Location of microfossil assemblage data analysed including data on 25 planktonic foraminifera (grey squares), 6 dinocyst (orange triangles) and 4 coccolithophore (blue circles) census count time series. Background colour gradient represents annual mean sea surface temperature (SST) from the World Ocean Atlas (WOA; Locarnini et al., 2019)

Although there are fewer dinocyst and coccolithophore than planktonic foraminifera time series, they also cover major parts of the latitudinal and thermal gradients in the North Atlantic Ocean (Figure 4-1). To ensure the chronological comparability of all analysed time series, we either used the revised age models that are 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 and Stern, 2016) as well as radiocarbon ages (see also Strack et al., 2022).

All plankton assemblage count data used here were taxonomically harmonised. Planktonic foraminifera assemblage data were harmonised following Siccha and Kucera (2017) (see Chapter 3.4.1 for a more detailed explanation). Dinocyst taxonomy was harmonised following de Vernal et al. (2020) with slight additions following Zonneveld et al. (2013). Names that could not be resolved using synonym lists and assigned a harmonised name following de Vernal et al. (2020) and Zonneveld et al. (2013) were treated as unidentified specimens and were excluded from the 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 (that is, zero abundance) which is in accordance with the completeness of the counts reported in the original studies. An average of 330 to 1250 planktonic foraminifera specimens, 320 to 480 coccoliths and 200 to 550 dinocysts were counted per sample and study, which are sufficient sample sizes to reliably determine relative abundances of each species (Phleger, 1960; Dennison and Hay, 1967; Al-Sabouni et al., 2007). The original data were either given in absolute or relative abundances, and we transformed them all to relative abundances based on the number of counted specimens. In total, 41 species of planktonic foraminifera, 30 species of coccolithophores and 53 species of organic-walled dinocysts were observed in our study (see Extended Data Table 4-2, Extended Data Table 4-3, and Extended Data Table 4-4 for full species lists).

### 4.2.2 Principal component analysis on species composition

We applied a principal component analysis (PCA) on the standardised assemblage data of each time series and extracted, for each time series, the first axis (which explains most variance in the assemblage data). To align all first principal component (PC) axes in the same direction, we checked and, if necessary, changed their polarisation by fitting linear models through all first PC axes.

### 4.2.3 Generalised additive models on species composition

We use generalised additive models (GAMs) on the individual first PC axes scores to estimate the overall trend in each plankton group. We interpolated the first PC scores at 0.5 kyr bins to adjust for the differences in the resolution of the individual records. To prevent edge effects, we also restricted the interpolated data to the interval that is covered by all time series corresponding to plankton groups (that is, 2.5-23 ka for planktonic foraminifera, 3.5-22.5 ka for coccolithophores and 3.5-23 ka for dinocysts). The advantage of using GAMs is that the complexity of the fitted model is determined objectively, because smoothing methods are applied automatically (Simpson, 2018). The significance of the individual GAMs 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 trend are estimated using centred finite differences and 95% across-the-function confidence intervals are calculated (see Simpson, 2018).

### 4.2.4 Sensitivity analysis

We conducted a sensitivity analysis to check whether our observed plankton signals might be the result of sampling bias, because the number of available time series for planktonic foraminifera is four to five times higher than the number of available time series for coccolithophores and dinocysts. For this, we re-sampled the planktonic foraminifera dataset and compiled two subsets with time series that are closest (geodesic distance) to the dinocyst and coccolithophore time series and re-calculated the overall trend (GAMs) and time periods of significant change (1st derivative of GAMs) for these two planktonic foraminifera subsets. The significance of the GAMs of these subsets are also given by associated F statistics and tests of the null hypothesis of no trend.

### 4.2.5 Spatio-temporal biodiversity change

To analyse the 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, i.e., the Last Glacial Maximum (LGM). Species gains and losses take species identity into account (Antão et al., 2020) and were calculated for each sample in a time series as the proportion of species that were 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).

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

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

where $S$ is the number of species at a specific site and $p_i$ is the relative abundance of the $i$-th species.

The rates of plankton biodiversity change were then quantified using calculated slopes of fitted linear models for species richness, gains, losses, and ENS (see Extended Data Figure 3-3, Extended Data Figure 3-4, and Chapter 3.4.4 for a more detailed explanation).

To get a better understanding of the spatio-temporal dynamics of plankton biodiversity, we further assessed the difference between species richness and ENS of each sample with the mean LGM species richness and ENS of the time series. The mean LGM species richness and ENS were determined for all samples that fall into the LGM interval (that is, 19-23 ka, as defined in Mix et al. (2001) and Kucera et al. (2005a)). These differences were then gridded in Hovmoller-like plots with a grid cell resolution in time and space of 1 kyr and 2.5°.

### 4.2.6 R packages

All statistical analyses were performed in R version 4.1.3 (R Core Team, 2024) using the ‘tidyverse’ packages (Wickham et al., 2019) and the ‘janitor’ package (Firke, 2023) for cleaning and importing the data; ‘codyn’ (Hallett et al., 2016; Hallett et al., 2020) and ‘car’ (Fox and Weisberg, 2019) package for community structure analyses; ‘FactoMineR’ (Lê et al., 2008) and 'factoextra' (Kassambara and 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) for the plots.

## 4.3 Results

We analysed 25 planktonic foraminifera, 6 dinocyst and 4 coccolithophore assemblage time series across the latitudinal gradient of the North Atlantic Ocean (Figure 4-1, Extended Data Table 4-1). In all three plankton groups, the first PC axes of the compositional change show a unidirectional response, with the first PC axes of the individual trends explaining 20-65% of the variance in planktonic foraminifera, 13-23% in dinocyst and 19-31% in coccolithophore time series (Figure 4-2). GAMs indicate that the response of all three groups is characterised by a compositional change trend, which is statistically significant (Table 4-1). 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 trend (Figure 4-2), reflecting the local response at each of the analysed sites.

**Table 4-1:** Summary statistic of fitted generalised additive models (GAMs) by plankton group with associated F-statistic and test of the null hypothesis of no trend (p value). R-sq. (adj): adjusted R-squared for the model; n: number of data points (samples); edf: estimated degrees of freedom. Planktonic foraminifera subsets I and II relate to the sensitivity analysis described in the Methods and Figure 4.

| Dataset | R-sq. (adj) | n | 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 = 4) | 0.358 | 156 | 2.645 | 32.27 | << 0.0001 |
| | | | | | |
| planktonic foraminifera subset I (n = 6) | 0.642 | 252 | 6.606 | 67.56 | << 0.0001 |
| planktonic foraminifera subset II (n = 4) | 0.621 | 168 | 4.799 | 56.5 | << 0.0001 |

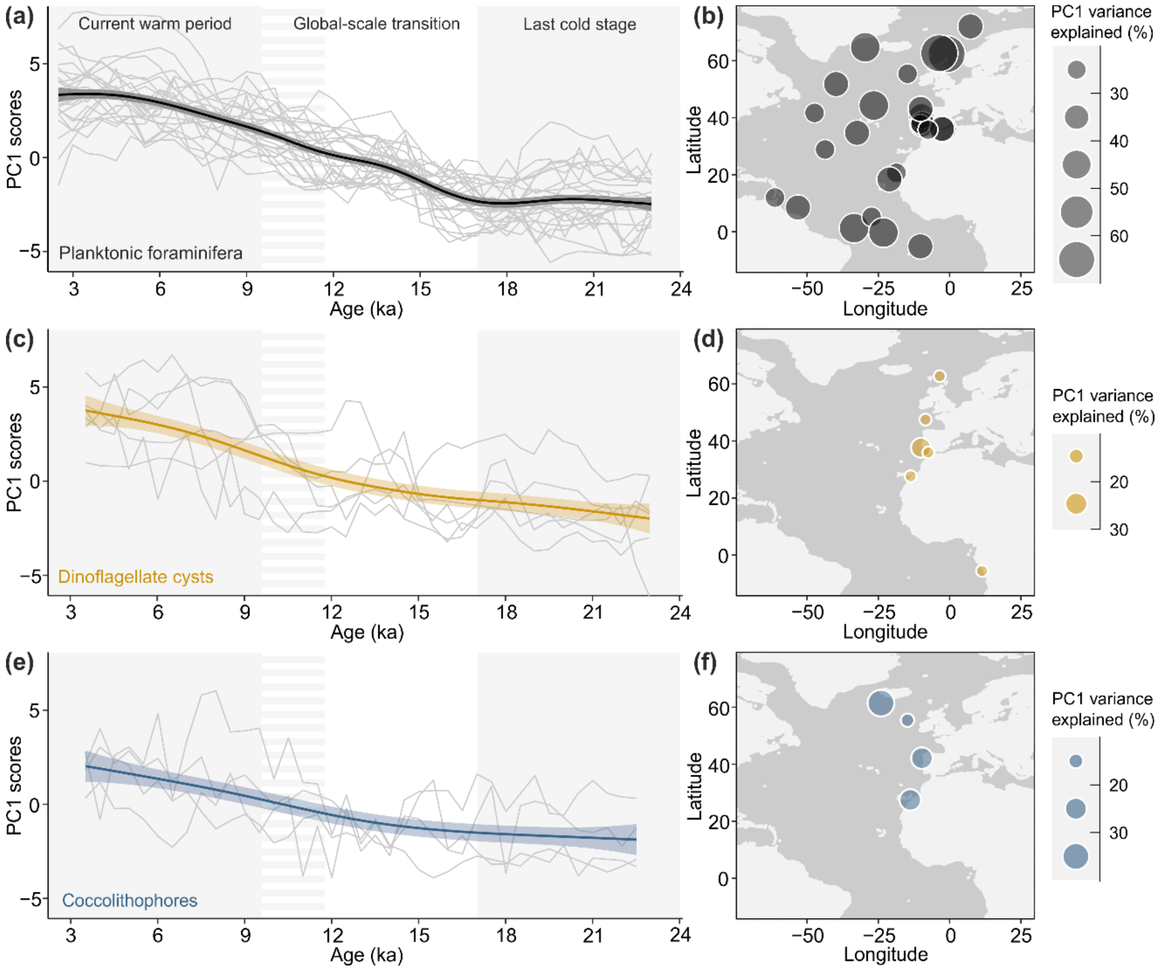


**Figure 4-2:** Compositional change in marine plankton groups during the past 24,000 years obtained from analysis of time series of census counts of three plankton groups: planktonic foraminifera (a,b, dark grey), dinocysts (c,d, orange) and coccolithophores (e,f, blue). (a,c,e) Compositional change within individual time series visualised as first principal component (PC1) axes scores (grey lines, interpolated at 0.5 kyr). Overall compositional change is shown as generalised additive model (GAM) fits (coloured lines) and their 95% confidence intervals (coloured shadings). (b,d,f) Amount of variance explained by each individual PC1 axis at the location of each time series.

Nevertheless, the overall pattern is robust and indicates that the time periods of significant change were similar in the three plankton groups (Figure 4-3). The shift in assemblage composition in all plankton groups started with the onset of the global-scale warming (16-17 ka ago) and the assemblages kept changing during the Holocene, at least until 4-5 ka

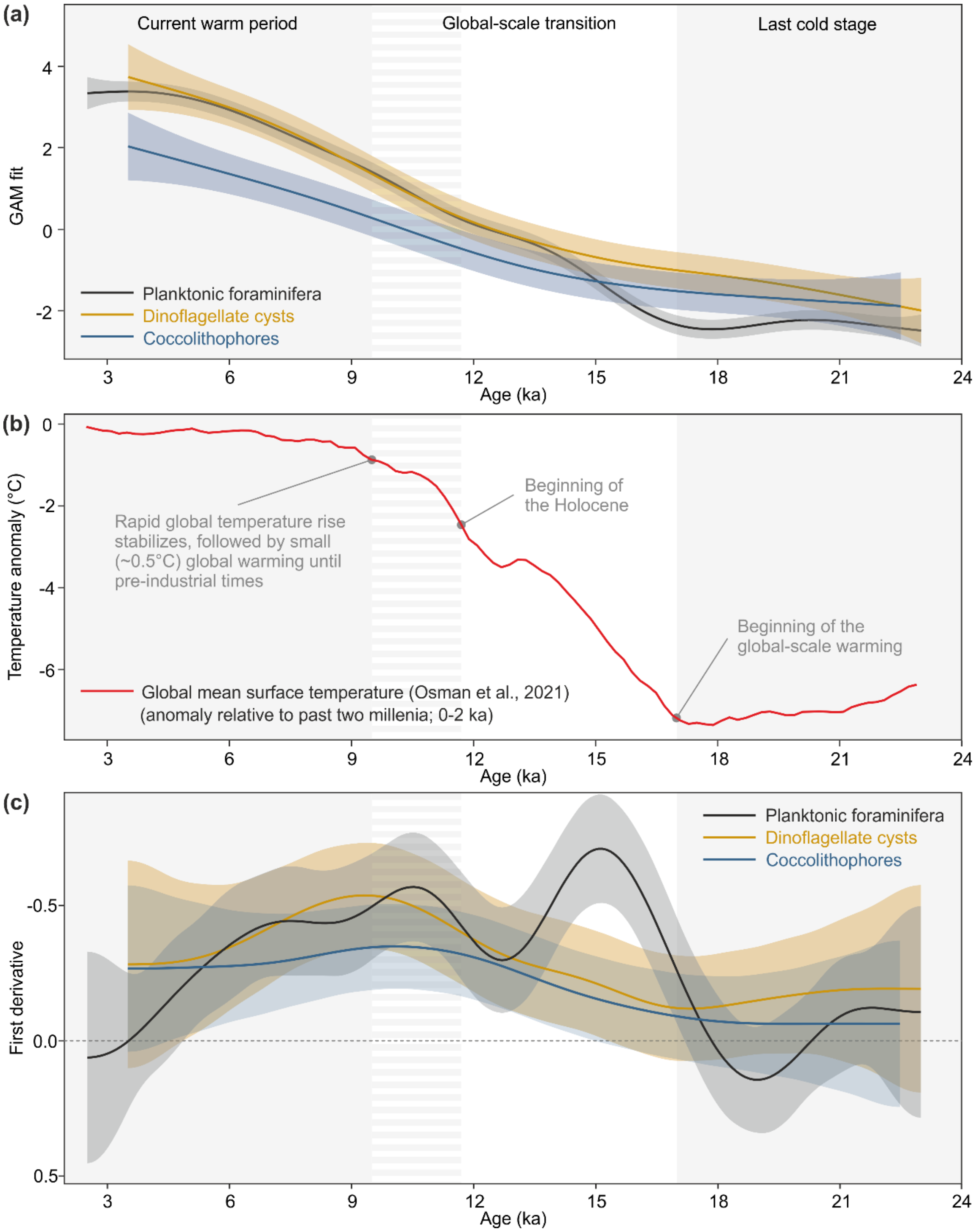


**Figure 4-3:** Marine plankton assemblage response to global warming during the past 24,000 years. (a) Overall compositional change shown as generalised additive model (GAM) fits (see also Figure 2) for planktonic foraminifera (dark grey), coccolithophores (blue) and dinocysts (orange) and their 95% confidence intervals (coloured shadings). (b) Development of 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 shadings).

ago (Figure 4-3c). Thus, all three plankton groups show substantial degree of continued assemblage change even during the current warm period, when global temperature forcing was low (Figure 4-3b; see Chapter 3 for more detailed planktonic foraminifera analyses). Because of the uneven sampling among the three plankton groups, we tested whether the overall trend of planktonic foraminifera (the group with most time series) is similar when subsampling time series closest to dinocyst and coccolithophore time series (6 and 4, respectively). This sensitivity analysis shows that the overall trend and the period of significant species compositional change in planktonic foraminifera are robust when considering sampling bias (Figure 4-4, Table 1). Thus, over the past 24 kyr, the main pattern of assemblage composition change in zoo- and phytoplankton appears similar.

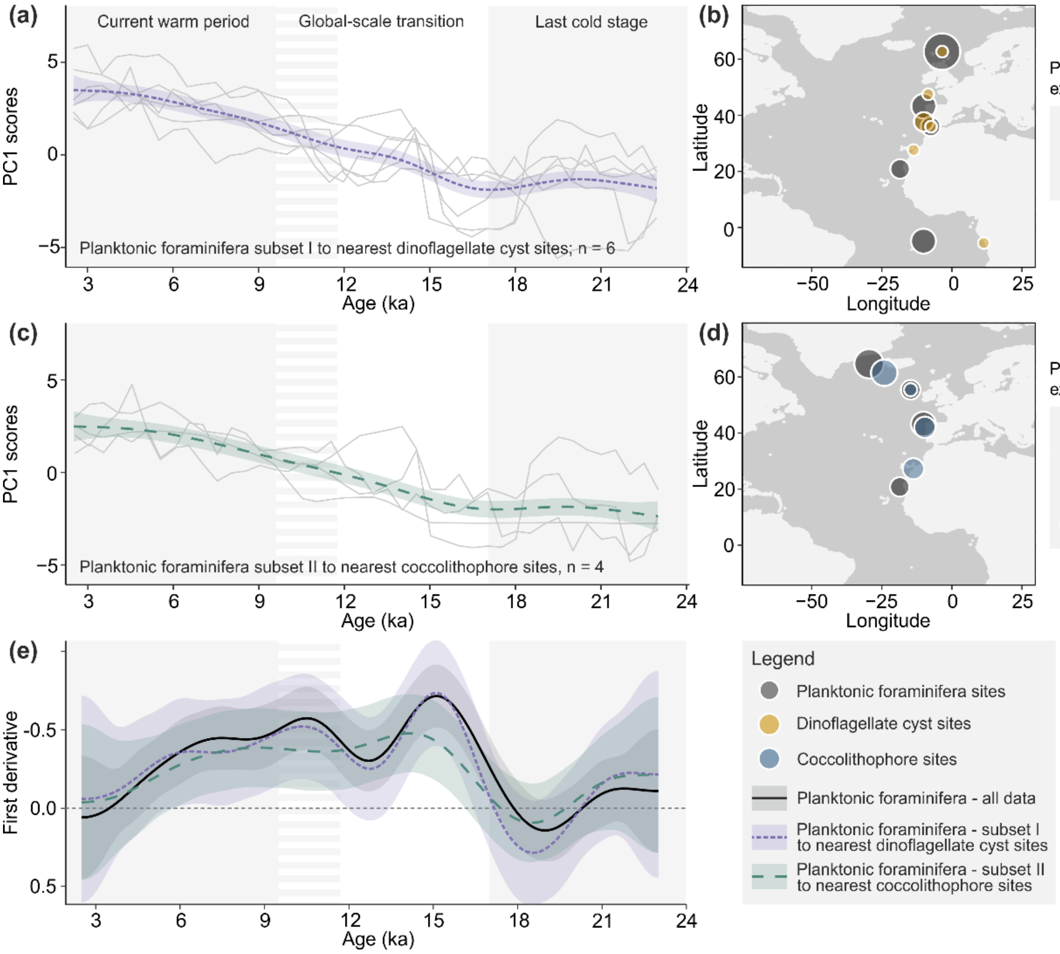


**Figure 4-4:** To check for sampling bias, the planktonic foraminifera dataset (Figure 2a,b) was re-sampled to only include the time series that are closest to the dinocyst records (a,b, subset I) and the coccolithophore records (c,d, subset II). (a,c) Compositional change within individual time series shown as first principal component (PC1) axes scores (grey lines, interpolated at 0.5 kyr) and overall compositional change shown as generalised additive model (GAM) fits (coloured lines) and their 95% confidence intervals (coloured shadings). (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 shadings).

To determine whether this similarity applies also to the individual components of assemblage change, in the next step, we compared changes in alpha-diversity, and species gains and losses (Figure 4-5). This analysis reveals that in all three groups, the largest change in species richness (and effective number of species) occurred in the mid-latitudes, while the lower latitudes remained relatively stable or showed a slight decrease species richness (Figure 4-5a,g). All plankton groups show an asymmetry in the gains and losses of species, with the magnitude of local immigration being higher than local extinctions (Figure 4-5c-f). We observe a higher accumulation of gained, new species in the mid-latitudes (Figure 4-5c) and relatively stable values in the lower latitudes, consistent with the local trends in richness. In contrast, species losses were highest in the lower latitudes, but exhibited a lower magnitude than species gains in the mid-latitudes (Figure 4-5e). We also see a decrease in the proportion of lost species in the mid-latitudes over the past 24 kyr (Figure 4-5e), meaning that most species that were present in this region during the LGM persisted throughout the deglaciation, but the community was progressively enriched by colonisation from the lower latitudes. Finally, we observe a consistent decrease in ENS in equatorial time series for all plankton groups over the past 24 kyr (Figure 4-5g), even though the change in species richness in the lower latitudes was low (Figure 4-5a), meaning that most species present in the lower latitudes during the LGM remained, but the dominance structure of the species in these assemblages changed through time. The median values of species richness, gains and losses are comparable among the different plankton groups (Figure 4-5b, d, f). However, the median ENS of dinocysts appears different when compared to planktonic foraminifera and coccolithophores (Figure 4-5h), probably caused by the relatively high spatial ENS variability in the analysed dinocyst time series (Figure 4-5g).

The spatio-temporal analysis of the biodiversity changes in the three plankton groups reveals that the large net surplus of species in the mid-latitudes started to accumulate at the end of the last deglaciation around 15 ka (Figure 4-6). The observed decrease in equatorial ENS (Figure 4-5g) started to evolve with the beginning of the current warm period around 12 ka and intensified in planktonic foraminifera and dinocysts towards the present (Figure 4-6). Interestingly, richness and ENS of dinocysts and coccolithophores seem to peak in the mid-latitudes between 6-9 ka ago followed by a steady decrease (Figure 4-6d-i). A similar alpha-diversity peak is not as clearly recognizable in the planktonic foraminifera time series, where we have more records in the mid-latitudes (Figure 4-6a-c).

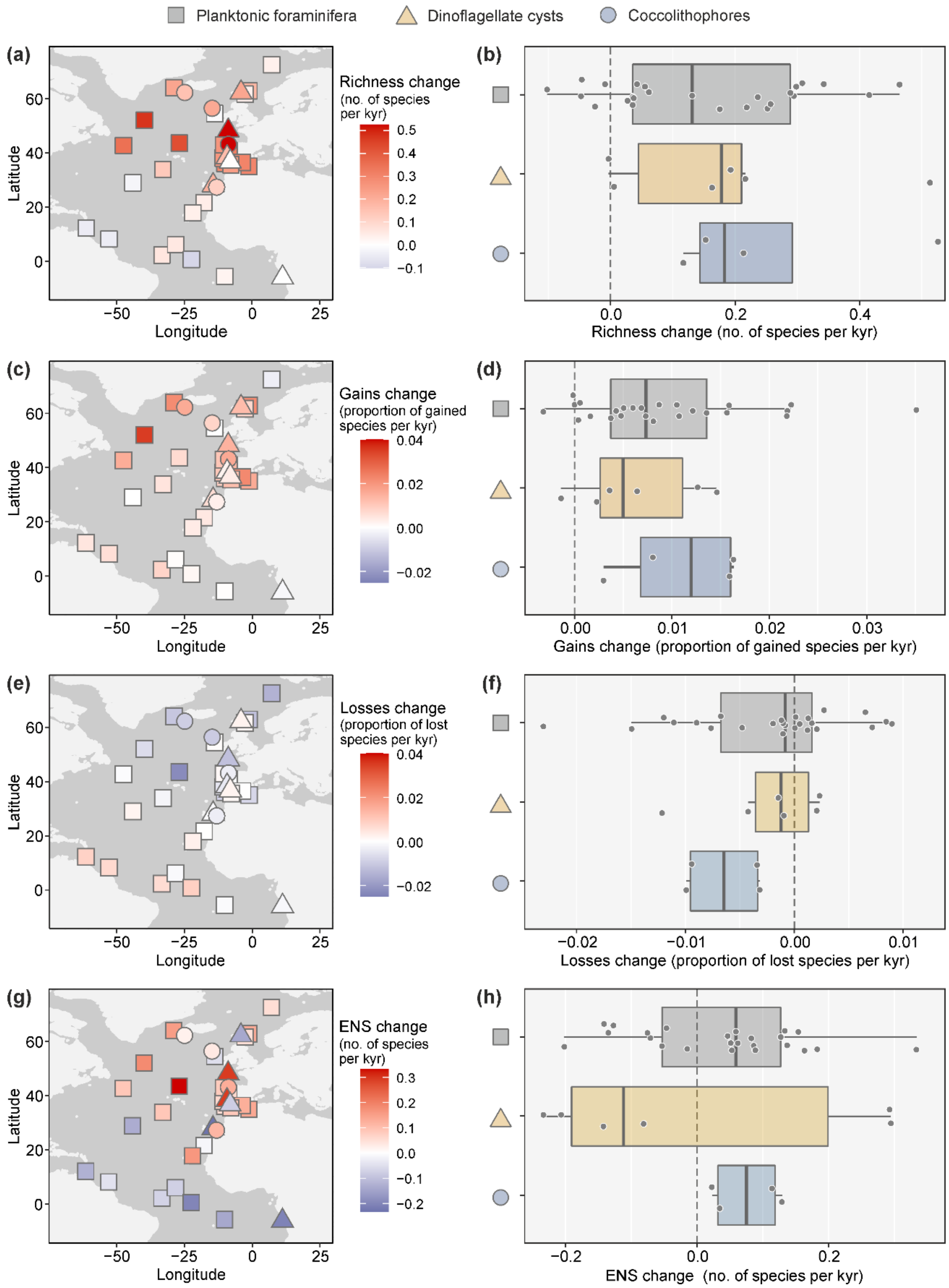


**Figure 4-5:** Local rates of biodiversity change of marine plankton during the past 24,000 years. Spatial distribution of rates of change in (a,b) species richness, the proportion of (c,d) gained and (e,f) lost species, and (g,h) the effective number of species (ENS) since the Last Glacial Maximum 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 Figure 3 and 4 of Strack et al., 2022). For example, a positive slope of richness (or ENS) change indicates a net increase in species number (or ENS) through time, a positive gains change indicates an accumulation of new species through time, and a positive losses change indicates that species losses are accumulating through 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-axes scales of the box plots.

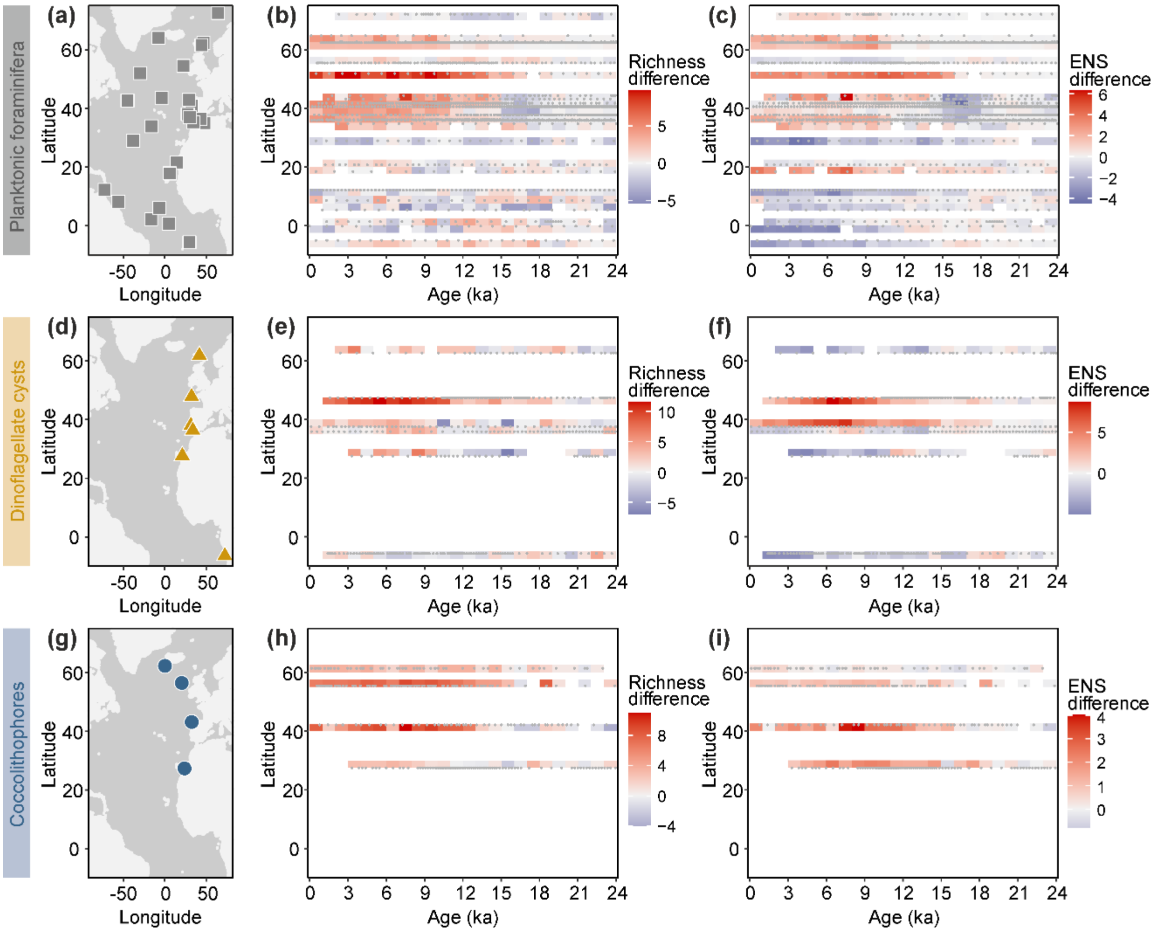


**Figure 4-6:** Spatio-temporal evolution of species alpha-diversity during the past 24,000 years. (a,d,g) Locations of individual time series per plankton group: planktonic foraminifera (grey squares), dinocysts (yellow triangles) and coccolithophores (blue circles). Differences in (b,e,h) species richness and (c,f,i) effective number of species (ENS) between each given sample and the Last Glacial Maximum (LGM) mean of each time series. Grid cells show the mean difference of the given samples at 1 kyr by 2.5° latitude resolution. Positive numbers (reddish colours) indicate the LGM richness or ENS was lower (i.e., increased with time), and negative numbers (blueish colours) indicate species richness or ENS decreased with time. Grey dots within the grids represent each individual sample.

## 4.4 Discussion

The joint analyses of assemblage composition time series in three groups of plankton reveal that the transformation of the marine environment associated with the global warming during the last deglaciation was accompanied by a significant response of marine plankton assemblages. Despite the large differences in the sampling, species diversity and ecology of planktonic foraminifera, dinocysts and coccolithophores, these three plankton groups show remarkably similar trends in assemblage change through time (Figure 4-3, Figure 4-5, Table 4-1). The onset of their response to climate change is similar, yet all three plankton groups show a pronounced non-linearity with climate change marked by a continued response into the Holocene despite low temperature forcing (Figure 4-3). Our sensitivity analysis (Figure 4-4) indicates that the similarity among the patterns is not affected by sampling bias, even though the number of included dinocyst and coccolithophore time series is four to five times lower than of included planktonic foraminifera time series and the dinocyst and coccolithophore time series have less spatial coverage (Figure 4-1).

In all three groups, the response to deglacial warming is characterised by a distinct long-lasting shift in species composition of the plankton assemblages (Figure 4-3), reflecting the dominance of poleward migration leading to an asymmetry between local immigration and extinction (Figure 4-5c-f) and a net surplus of species in the mid-latitudes (Figure 4-5a). Although the species richness in the tropics during the past 24 kyr remained relatively stable (Figure 4-5a), there is a consistent drop in ENS in these equatorial time series during the Holocene (Figure 4-6). Thus, even though there were few or none local species extinctions after the deglaciation, some equatorial species became more dominant leading to less diverse (lower ENS) assemblages. The observed decrease in equatorial ENS might, therefore, suggest that some equatorial plankton species already reached the maximum of their thermal ranges in the Holocene and are decreasing in abundance since then, rendering equatorial plankton biodiversity vulnerable to continued global warming. Indeed, recent loss in tropical species richness has been described for many pelagic and benthic chordates and benthic invertebrates such as gastropods, bivalves and arthropods (Chaudhary et al., 2021) and is predicted for reef corals (Kiessling et al., 2012), planktonic foraminifera (Yasuhara et al., 2020b) and marine species in general (Brown et al., 2022; Hodapp et al., 2023). Thus, our findings provide support for the prediction that current and future warming of the oceans will lead to an intensification of the reshuffling of the marine flora and fauna resulting in the extinction of endemic polar species and a severe decline of tropical diversity and species richness (Yasuhara and Deutsch, 2022).

In all three groups of plankton, a large part of the observed assemblage composition change occurred during the climatically comparably stable Holocene (Figure 4-3c). Assemblages continued to change until at least 4-5 ka at the same rate as they did during the deglaciation, despite the fact that the rate of global warming changed at the start of the current warm period (around 11 ka, Figure 4-3b). This compositional change observed during a climatically stable period could be a result of delayed species response to the deglaciation (extinction lag), or it could mean that factors other than temperature drove changes in species composition during this period, such as other abiotic factors, neutral drift, new ecological interactions, or species adaptation to new local conditions.

Neutral drift, i.e., stochastic changes in species abundance that happen at any given time (Vellend, 2010), is likely only a minor contributor the observed plankton assemblage change because the population size of the plankton groups is large and the strong climatic forcing during the last deglaciation should override any effects of neutral drift (Vellend, 2010). If neutral drift would be the main contributor to the assemblage change during the last 24 kyr, we would also expect a significant assemblage change during the last cold stage (before 18 ka) that was climatically more stable than the deglaciation, which is not the case (Figure 4-3c). Also, since the observed continued change is consistent among the plankton groups (e.g. poleward migration of species, decline in equatorial ENS), underlying selective processes are more likely than purely stochastic processes as a cause for the similarity in the observed patterns in the plankton groups.

Extinction lag, i.e., a long lag between the extinction-committed climate forcing event (the last deglaciation) and the final disappearance of species' (Jackson and Sax, 2010), is also unlikely to be the reason for the prolonged assemblage change in the Holocene. The net surplus of species in the mid-latitudes during the past 24 kyr is not a short transient phenomenon but persists for several millennia (Figure 4-6) and we observe no continuous species losses during the middle to late Holocene in the mid-latitudes that would indicate extinction 'payoff' within the investigated time interval (Extended Data Figure 4-1). Thus, if extinction lag would be a main driver of the compositional change during the Holocene, it would be a long delay/memory effect of several thousand years and mean that cold-water adapted species have a very delayed response to the warming (longer than the time period of the Holocene investigated in this study). Even though, long lags have been described for tree species and large mammals (Williams et al., 2021), we expect faster response times in marine plankton due to their short life-cycle, a lack of barriers in the ocean and high dispersal potential due to currents. We further document a rapid response of the planktonic foraminifera assemblages to a short-lived cold interval (Heinrich Event I; Broecker, 1994; Figure 4-6b,c) , showing that any lags in plankton assemblage change in response to climate change are likely shorter than a millennium.

Even though sea surface temperature is thought to be the main predictor in the distribution and diversity of the investigated plankton groups (Rutherford et al., 1999; Esper and Zonneveld, 2002; Morey et al., 2005; Taylor et al., 2008; Chen et al., 2011a; Charalampopoulou et al., 2016; Fenton et al., 2016b; O'Brien et al., 2016; Rillo et al., 2021), it is surely not the sole environmental driver (e.g. Hohmann et al., 2020; Rillo et al., 2021). Since all plankton groups responded coherently to the temperature forcing during the last deglaciation, we assume that this large temperature change overwhelmed other (environmental) changes during that time period. Nevertheless, other abiotic factors may also drive changes in plankton biogeography, especially in the lower latitudes (Rillo et al., 2021) and in the current warm period where temperature forcing is lower compared to the deglaciation. For instance, insolation changes during the current warm period led to a lower magnitude of seasonal temperature range and a lesser degree of water column stratification from the mid to late Holocene which influence plankton biogeography and diversity (Berger and Loutre, 1991; Solignac et al., 2006). However, due to the differences in ecological preferences of the studied plankton groups, we would also expect a difference in the response of the plankton groups during the Holocene, which is not the case.

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 into new habitats (Figure 3-1b) and the persistence of the original species in these habitats (Figure 4-6) caused the formation of novel assemblages after the last deglaciation (Figure 3-4), in which new direct and indirect interspecific ecological interactions emerged. For the investigated plankton groups in particular, these might be changes in grazing pressure (all groups), changes in food availability (planktonic foraminifera and some dinoflagellates 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 selective pressure on all groups and possibly drive assemblage change and local adaptation (Liow et al., 2011; Brockhurst et al., 2014).

The observed prolonged plankton assemblage change from the beginning of the Holocene until at least 4-5 ka (Figure 4-3c), might therefore indicate a shift in the dominant drivers of plankton assemblage change from more abiotic-dominated causes (that is, environmental forcing) during the last deglaciation to more biotic-dominated causes. Such a shift in the dominant driver of assemblage change was also described for a 24 kyr record of terrestrial plants by Doncaster et al. (2023). They found that abiotic forcing (i.e., temperature) was the main driver of community assembly until around 9 ka ago, while internal processes (i.e., competition, niche construction) dominated community assembly until the present. So, the reduced environmental forcing, species migration and the resulting novel ecological interactions led to a large-scale readjustment of the plankton community to the warm conditions after the onset of the current warm period. Since these novel ecological interactions are a consequence of the environmental forcing during the last deglaciation, the prolonged assemblage change is possibly indirectly linked to the preceding climatic forcing. In this hypothesis, plankton response to large-magnitude unidirectional climate change would be characterised by a cascade of direct response by asymmetric range shifts, leading to the establishment of novel communities and interactions, followed by subsequent community transformation under reduced environmental forcing due to biotic interactions in the new communities.

## 4.5 Conclusion

The present study was conducted to reveal the spatio-temporal biodiversity patterns of planktonic foraminifera, dinocysts and coccolithophores in the North Atlantic Ocean throughout the past 24 kyr. Based on our data the following conclusions can be drawn:

(1) Zoo- as well as phytoplankton assemblages were significantly affected by the last deglaciation and show comparable large-scale patterns in local biodiversity and overall assemblage response despite differences in the ecology, diversity and number of time series analysed among the different plankton groups.

(2) All plankton groups show a significant assemblage change lasting from the onset of the last global warming at 16-17 ka ago until at least 4-5 ka ago, therefore, post-dating the end of the last deglaciation and the rapid global warming by several millennia (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.

We show that zoo- and phytoplankton were affected by the last deglaciation, which is in its magnitude comparable to future projected global warming (Jackson and Overpeck, 2000). Nevertheless, the major portion of the environmental change during the past 24 kyr happened over a course of at least 6,000 years, whereas the future global warming is expected to happen over a much shorter time period. In addition, after the last deglaciation cold-adapted taxa were confronted with warm conditions, whereas in the future warm-adapted taxa will be confronted with even warmer conditions. So, even though this study reveals how the plankton community responded to environmental change analogous in magnitude to the projected future warming, the question remains whether plankton communities will cope with a more rapid global warming in the same way. This is especially so considering the potentially significant role of biotic interactions in the observed response cascade.

## Data availability

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 Supportive Information Table S1 (coccolithophore assemblage data publication to PANGAEA in process).

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/).

Taxonomically harmonized planktonic foraminifera assemblage data are available at https://zenodo.org/record/6948750 and taxonomically harmonized dinocyst and coccolithophore assemblage data will also be made available prior to publication.

## Code availability

The R code used to generate the results of this study will be made available prior to publication.

## Acknowledgements

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## 4.6 Extended Data

### Sample preparation for coccolithophore assemblage data

Coccolithophore assemblage data is based on the counting of individual coccoliths. Samples were analysed at 2-32 cm intervals for 162-984C, 1-30 cm intervals for 162-980, 0.5-10 cm intervals for GeoB11035-1 and 4-10 cm intervals for GeoB5546-2. The sediment samples were prepared using a combined dilution/filtering technique as described by Andruleit (1996). Since this technique is fast and easy to apply, an alteration of the coccoliths due to fragmentation or dissolution is minimal. Between 50 and 100 mg dry bulk sediment was brought into suspension using demineralized water buffered with ammonia (pH ~ 8.5-9). The suspension was ultrasonicated for 15 to 30 s to homogenize the samples and break small sediment lumps. Afterwards, the suspension was split (split factor = 100) using a rotary splitter and filtered onto polycarbonate membrane filters (0.4 µm pore size) using a vacuum pump. The samples then have been dried at 40°C for 24 h before ~1x1 cm filter aliquots were mounted on an aluminium stub that was prepared with electroconductive, self-adhesive, carbon-based discs (PLANO Leit tabs). Finally, the mounted samples were sputtered with gold/palladium in a Polaron SC7640 Sputter Coater. Where possible, a minimum of 300 coccoliths were counted under a Zeiss DSM 940A scanning electron microscope at 3,000x or 5,000x magnification. In some samples fewer coccoliths have been counted due to very low abundances (total coccolith counts are given for all samples). Coccolith counts were then converted into numbers of specimens per gram dry bulk sediment.

**Extended Data Table 4-1:** Details of the 35 studied time series and corresponding data references

| | | Lat. | Long. | Depth | Res. | Assemblage data | | Metadata used for age models | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | **Site** | (°N) | (°E) | (m) | (kyr) | Reference | Data | 14C ref. | 14C data | Iso ref. | Iso data |
| Planktonic foraminifera | **GIK17730-4** | 72.11 | 7.39 | -2749 | 0.63 | Schulz (1995a) | Schulz (1995b) | Sarnthein et al. (1995) | Sarnthein (2003) | - | - |
| | **V28-14** | 64.78 | -29.57 | -1855 | 1.31 | CLIMAP Project Members (1981) | CLIMAP Project Members (2009) | * | | | |
| | **MD99-2285** | 62.69 | -3.57 | -885 | 0.58 | Wary et al. (2017) | ** | Wary et al. (2017) | ** | - | - |
| | **MD99-2284** | 62.37 | -0.98 | -1500 | 0.04 | Eldevik et al. (2014) | Dokken et al. (2015) | Rasmussen et al. (2006); Svensson et al. (2008); Bakke et al. (2009); Risebrobakken et al. (2011); Dokken et al. (2013) | ** | - | - |
| | **162-980** | 55.48 | -14.70 | -2180 | 0.23 | Benway et al. (2010) | Benway et al. (2013) | * | | | |
| | **SU90-I03** | 51.88 | -39.78 | -2970 | 0.96 | Schulz (1995a) | Schulz (1995c) | - | - | Schulz (1995a) | Schulz (1995d) |
| | **GIK15612-2** | 44.36 | -26.54 | -3050 | 0.63 | Kiefer (1998) | Kiefer and Sarnthein (1998) | * | | | |
| | **SU92-03** | 43.20 | -10.11 | -3005 | 0.67 | Salgueiro et al. (2010b) | Salgueiro et al. (2010a) | Salgueiro et al. (2010b) | ** | Salgueiro et al. (2010b) | Salgueiro et al. (2010c) |
| | **CH69-K09** | 41.76 | -47.35 | -4100 | 0.18 | Labeyrie et al. (1999) | Labeyrie et al. (2017) | * | | | |
| | **MD95-2040** | 40.58 | -9.86 | -2465 | 0.15 | de Abreu et al. (2003a) | de Abreu et al. (2003b) | * | | | |
| | **MD95-2041** | 37.83 | -9.51 | -1123 | 0.34 | Voelker and de Abreu (2011b) | Voelker and de Abreu (2011a) | Voelker and de Abreu (2011b) | Voelker and de Abreu (2011c) | Voelker et al. (2009a) | Voelker et al. (2009b) |
| | **MD95-2042** | 37.80 | -10.17 | -3146 | 0.27 | Chabaud et al. (2014) | Rossignol (2022) | Chabaud et al. (2014) | ** | Cayre et al. (1999a) | Cayre et al. (1999b) |
| | **MD95-2043** | 36.14 | -2.62 | -1841 | 0.26 | Pérez-Folgado et al. (2003e) | Pérez-Folgado et al. (2003b) | * | | | |
| | **161-977A** | 36.03 | -1.96 | -1984 | 0.56 | Pérez-Folgado et al. (2003e) | Pérez-Folgado et al. (2003a) | Pérez-Folgado et al. (2003e) | Pérez-Folgado et al. (2003d) | Pérez-Folgado et al. (2003e) | Pérez-Folgado et al. (2003c) |
| | **MD99-2339** | 35.89 | -7.53 | -1177 | 0.19 | Eynaud et al. (2009); Voelker and de Abreu (2011b) | Voelker et al. (2010) | * | | | |
| | **V32-8** | 34.78 | -32.42 | -3252 | 0.95 | Mix (1986) | Mix (2006e) | - | - | Mix (1986) | Mix (1999a) |
| | **V22-222** | 28.93 | -43.65 | -3197 | 0.83 | Mix (1986) | Mix (2006a) | - | - | Mix et al. (1986a) | Mix et al. (1986b) |
| | **108-658C** | 20.75 | -18.58 | -2273 | 0.59 | Haslett and Smart (2006) | - | deMenocal et al. (2000a) | deMenocal et al. (2000b) | - | Knaack and Sarnthein (2005) |
| | **V30-49** | 18.43 | -21.08 | -3093 | 1.02 | Mix (1986) | Mix (2006d) | Mix and Ruddiman (1985) | CLIMAP Project Members (2004d) | Mix (1986); (1989) | Ruddiman (1997); Mix (2003c) |
| | **M35003-4** | 12.09 | -61.24 | -1299 | 0.31 | Hüls (2000) | Hüls (1999) | * | | | |
| | **V25-75** | 8.58 | -53.17 | -2743 | 0.81 | Mix (1986) | Mix (2006c) | Mix and Ruddiman (1985) | (CLIMAP Project Members, 2004a) | Mix (1986) | Mix (1999b, 2003a) |
| | **V30-36** | 5.35 | -27.32 | -4245 | 1.02 | Mix et al. (1999d) | Mix et al. (1999b) | Mix and Ruddiman (1985) | CLIMAP Project Members (2004b) | Mix (1986) | Mix (2003b) |
| | **V25-59** | 1.37 | -33.48 | -3824 | 0.75 | Mix (1986) | Mix (2006b) | * | | | |
| | **V30-40** | -0.20 | -23.15 | -3706 | 0.99 | Mix et al. (1999d) | Mix et al. (1999c) | Mix and Ruddiman (1985) | CLIMAP Project Members (2004c) | McIntyre et al. (1989) | McIntyre and Imbrie (2000) |
| | **RC24-16** | -5.04 | -10.19 | -3543 | 0.83 | Mix et al. (1999d) | Mix et al. (1999a) | - | - | McIntyre et al. (1989) | Imbrie and McIntyre (2000) |
| Dinocysts | **MD99-2285** | 62.69 | -3.57 | -885 | 0.67 | Wary et al. (2017) | ** | Wary et al. (2017) | ** | - | - |
| | **MD95-2002** | 47.45 | -8.53 | -2174 | 0.26 | Zaragosi et al. (2001) | Eynaud (1999) | Eynaud et al. (2007a) | Eynaud et al. (2007b) | - | - |
| | **339-U1385** | 37.57 | -10.13 | -2587 | 0.43 | Datema et al. (2019) | ** | - | - | Hodell et al. (2015a) | Hodell et al. (2015b) |
| | **MD99-2339** | 35.89 | -7.53 | -1177 | 0.38 | Penaud et al. (2011) | ** | * | | | |
| | **GeoB5546-2** | 27.54 | -13.74 | -1172 | 0.59 | Holzwarth et al. (2010a) | Holzwarth et al. (2009) | Holzwarth et al. (2010a) | Holzwarth et al. (2010b) | Holzwarth et al. (2010a) | Holzwarth et al. (2010c) |
| | **KZAI-01** | -5.70 | 11.23 | -816 | 0.24 | Hardy et al. (2016) | ** | Hardy et al. (2016) | ** | - | - |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Coccolithophores | **162-984C** | 61.43 | -24.08 | -1649 | 0.46 | Baumann, this study | *** | * | | | |
| | **162-980** | 55.48 | -14.70 | -2180 | 0.32 | Baumann, this study | *** | * | | | |
| | **GeoB11035-1** | 42.17 | -9.66 | -2045 | 0.49 | Baumann, this study | *** | Bender et al. (2012a) | Bender et al. (2012b) | - | - |
| | **GeoB5546-2** | 27.54 | -13.74 | -1172 | 0.25 | Baumann, this study | *** | Holzwarth et al. (2010a) | Holzwarth et al. (2010b) | Holzwarth et al. (2010a) | Holzwarth et al. (2010c) |

*age model from PALMOD 130k marine palaeoclimate data synthesis V1.1 (Jonkers et al., 2020) was used

**from paper/s or online supplements

***data publication at PANGAEA in process

**Extended Data Table 4-2:** Species list of observed planktonic foraminifera. The harmonised planktonic foraminifera taxonomy follows Siccha and Kucera (2017).

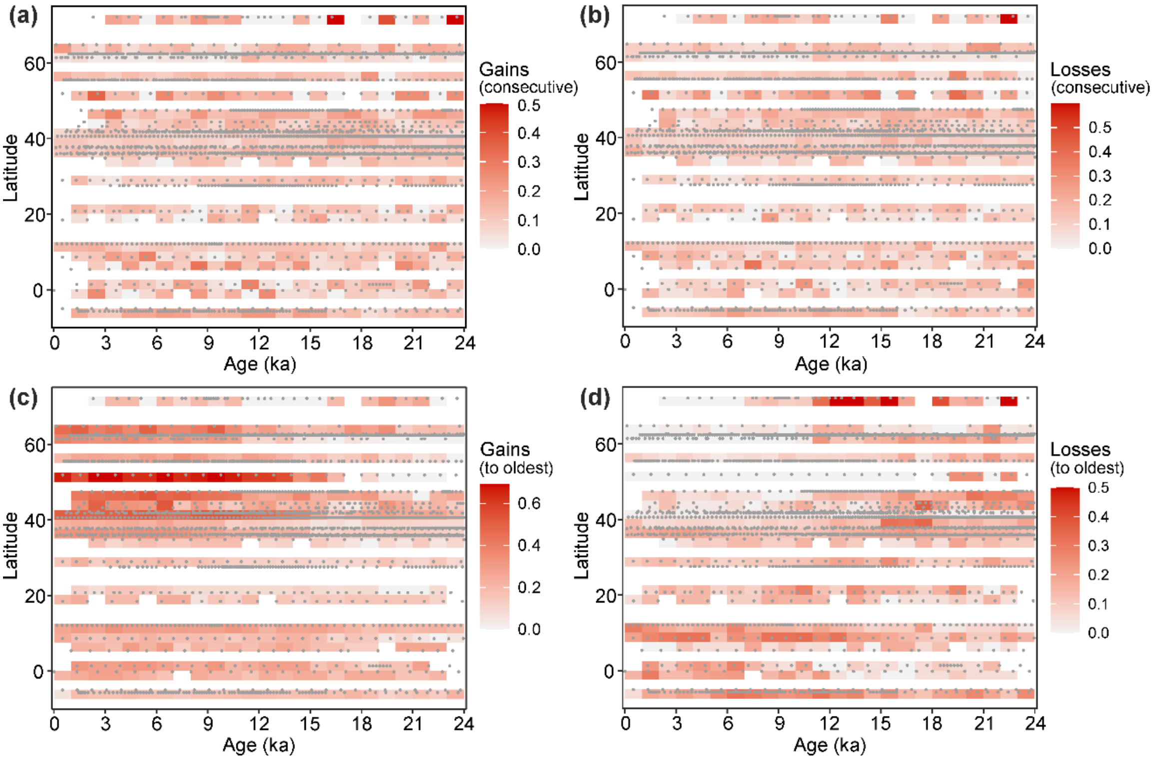
| | **Planktonic foraminifera** |
|---|---|
| **1** | *Beella digitata* |
| **2** | *Berggrenia pumilio* |
| **3** | *Candeina nitida* |
| **4** | *Dentigloborotalia anfracta* |
| **5** | *Globigerina bulloides* |
| **6** | *Globigerina falconensis* |
| **7** | *Globigerinella adamsi* |
| **8** | *Globigerinella calida* |
| **9** | *Globigerinella siphonifera* |
| **10** | *Globigerinita glutinata* |
| **11** | *Globigerinita minuta* |
| **12** | *Globigerinita uvula* |
| **13** | *Globigerinoides conglobatus* |
| **14** | *Globigerinoides ruber* |
| **15** | *Globigerinoides tenellus* |
| **16** | *Globoconella inflata* |
| **17** | *Globoquadrina conglomerata* |
| **18** | *Globorotalia cavernula* |
| **19** | *Globorotalia crassaformis* |
| **20** | *Globorotalia hirsuta* |
| **21** | *Globorotalia menardii* |
| **22** | *Globorotalia scitula* |
| **23** | *Globorotalia theyeri* |
| **24** | *Globorotalia truncatulinoides* |
| **25** | *Globorotalia tumida* |
| **26** | *Globorotalia ungulata* |
| **27** | *Globorotaloides hexagonus* |
| **28** | *Globoturborotalita rubescens* |
| **29** | *Hastigerina pelagica* |
| **30** | *Hastigerinella digitata* |
| **31** | *Neogloboquadrina dutertrei* |
| **32** | *Neogloboquadrina incompta* |
| **33** | *Neogloboquadrina pachyderma* |
| **34** | *Orbulina universa* |
| **35** | *Pulleniatina obliquiloculata* |
| **36** | *Sphaeroidinella dehiscens* |
| **37** | *Tenuitella iota* |
| **38** | *Tenuitella parkerae* |
| **39** | *Trilobatus sacculifer* |
| **40** | *Turborotalita humilis* |
| **41** | *Turborotalita quinqueloba* |

**Extended Data Table 4-3:** Species list of observed dinocysts. The harmonised dinocyst taxonomy follows de Vernal et al. (2020) with slight additions following Zonneveld et al. (2013).

| | **Dinocysts** |
|---|---|
| **1** | *Achomosphaera* spp. |
| **2** | *Ataxiodinium choanum* |
| **3** | *Bitectatodinium spongium* |
| **4** | *Bitectatodinium tepikiense* |
| **5** | *Brigantedinium* spp. |
| **6** | *Echinidinium aculeatum* |
| **7** | *Echinidinium delicatum* |
| **8** | *Echinidinium granulatum* |
| **9** | *Echinidinium karaense* |
| **10** | *Echinidinium* spp. indet. |
| **11** | Cyst of *Gymnodinium* sp. |
| **12** | *Impagidinium aculeatum* |
| **13** | *Impagidinium pallidum* |
| **14** | *Impagidinium paradoxum* |
| **15** | *Impagidinium patulum* |
| **16** | *Impagidinium plicatum* |
| **17** | *Impagidinium sphaericum* |
| **18** | *Impagidinium strialatum* |
| **19** | *Impagidinium velorum* |
| **20** | *Islandium minutum* |
| **21** | *Lejeunecysta* spp. |
| **22** | *Lingulodinium machaerophorum* |
| **23** | *Melitasphaeridium* spp. |
| **24** | *Nematosphaeropsis labyrinthus* |
| **25** | *Operculodinium centrocarpum* |
| **26** | *Operculodinium israelianum* |
| **27** | *Operculodinium janduchenei* |
| **28** | Cyst of *Pentapharsodinium dalei* |
| **29** | Cyst of *Polykrikos kofoidii* |
| **30** | Cyst of *Polykrikos schwartzii* |
| **31** | *Polysphaeridium zoharyi* |
| **32** | Cyst of *Protoperidinium americanum* |
| **33** | Cyst of *Protoperidinium monospinum* |
| **34** | Cyst of *Protoperidinium stellatum* |
| **35** | *Pyxidinopsis reticulata* |
| **36** | *Quinquecuspis concreta* |
| **37** | Cyst of *Scrippsiella trifida* |
| **38** | *Selenopemphix nephroides* |
| **39** | *Selenopemphix quanta* |
| **40** | *Spiniferites bentorii* |
| **41** | *Spiniferites delicatus* |
| **42** | *Spiniferites elongatus* |
| **43** | *Spiniferites* sp. granular type |
| **44** | *Spiniferites lazus* |
| **45** | *Spiniferites membranaceus* |
| **46** | *Spiniferites mirabilis* |
| **47** | *Spiniferites ramosus* |
| **48** | *Spiniferites* spp. indet. |
| **49** | *Trinovantedinium applanatum* |
| **50** | *Tuberculodinium vancampoae* |
| **51** | *Votadinium calvum* |
| **52** | *Votadinium spinosum* |
| **53** | *Xandarodinium xanthum* |

**Extended Data Table 4-4:** Species list of observed coccolithophores. The harmonised coccolithophore taxonomy follows Young et al. (2003).

| **Coccolithophores** | | | |
|---|---|---|---|
| **1** | *Acanthoica quattrospina* | **16** | *Helicosphaera wallichii* |
| **2** | *Algirosphaera robusta* | **17** | *Oolithotus antillarum* |
| **3** | *Calcidiscus leptoporus* subsp. *leptoporus* | **18** | *Oolithotus fragilis* |
| **4** | *Calcidiscus leptoporus* subsp. *quadriperforatus* | **19** | *Papposphaera* spp. |
| **5** | *Calciosolenia brasiliensis* | **20** | *Pontosphaera* spp. |
| **6** | *Coccolithus pelagicus* | **21** | *Reticulofenestra sessilis* |
| **7** | *Coronosphaera mediterranea* | **22** | *Rhabdosphaera clavigera* |
| **8** | *Emiliania huxleyi* | **23** | *Syracosphaera pulchra* |
| **9** | *Florisphaera profunda* | **24** | *Syracosphaera* sp. |
| **10** | *Gephyrocapsa ericsonii* | **25** | *Umbilicosphaera foliosa* |
| **11** | *Gephyrocapsa muellerae* | **26** | *Umbilicosphaera hulburtiana* |
| **12** | *Gephyrocapsa oceanica* | **27** | *Umbellosphaera irregularis* |
| **13** | *Gladiolithus flabellatus* | **28** | *Umbilicosphaera sibogae* |
| **14** | *Hayaster perplexus* | **29** | *Umbellosphaera tenuis* |
| **15** | *Helicosphaera carteri* | **30** | *Umbellosphaera* sp. |



**Extended Data Figure 4-1:** Spatio-temporal evolution of gains and losses during the past 24,000 years. For the gains and losses calculation, all samples in a time series are compared between (a,b) consecutive time points or (c,d) to the oldest sample in that time series (see Extended Data Figure 3 and Chapter 3.4 for a more detailed explanation). Grid cells show the mean difference of the given samples at 1 kyr by 2.5° latitude resolution and grey dots within the grids represent each individual sample. Planktonic foraminifera, dinocyst and coccolithophore time series are combined in each panel.

# 5 Manuscript III

## Investigating Holocene planktonic foraminifera assemblage change in the North Atlantic Ocean

**T. Strack, L. Jonkers, and M. Kucera**
Manuscript in preparation for submission

### Abstract

Marine biodiversity faces significant threats from current and future global warming. To understand species responses to climate change, fossil records offer a unique opportunity to study past environmental shifts. Planktonic foraminifera, abundant calcifying zooplankton with well-preserved sedimentary records, are essential in studying biogeographic patterns and biodiversity-climate relationships. In a previous study, we observed prolonged overall planktonic foraminifera assemblage change during the current warm period despite an overall low temperature forcing. In this study, we explore if this response is detectable on the local scale by comparing planktonic foraminifera assemblage change with local sea surface temperature (SST) during the Holocene. Additionally, we use planktonic foraminifera-derived SST to estimate how much assemblage change could be in theory explained by temperature change assuming uniformitarianism, meaning that the relationship between planktonic foraminifera assemblage change and SST has not changed over time. Our results indicate that local SST reconstructions might underestimate true local SST change during the Holocene and suggest that the relationship between planktonic foraminifera assemblage change and SST has changed within the last 24,000 years. These findings confirm our initial observation that a considerable amount of

observed assemblage change in the North Atlantic Ocean during the current warm period cannot be explained by SST alone.

## 5.1 Introduction

Marine biodiversity is already affected by current global warming on a global scale (Antão et al., 2020) and is expected to be even more affected by future anthropogenic global warming (Beaugrand et al., 2015; García Molinos et al., 2016). Understanding the threat that future global warming poses on the marine realm is an important yet challenging task, because it is difficult to predict how communities will respond to future anthropogenic warming. Observational data can help with these predictions, but rarely span more than 100 years (Dornelas et al., 2018), thus, only observing relatively small environmental change compared to the expected magnitude of future anthropogenic global warming. To overcome this obstacle, the fossil record of marine plankton can be utilised to better understand how marine species responded to environmental change that is comparable in its magnitude to expected future change. Indeed, the sedimentary record of eukaryotic marine microplankton has been proven sufficient to study the response of species to past climate change (Yasuhara et al., 2020a).

Within the realm of marine microplankton, planktonic foraminifera - prolific calcifying zooplankton that inhabit the upper water column - have one of the most complete sedimentary records (Aze et al., 2011). Planktonic foraminifera play a crucial role in palaeoceanography and palaeoecology, because their fossils have been successfully used to investigate biogeography patterns (Yasuhara et al., 2012b; Yasuhara et al., 2020b) and the relationship between biodiversity and past climate (Ezard et al., 2011; Fenton et al., 2016a). In a previous study (Chapter 3) we used the fossil record of planktonic foraminifera to show that overall plankton assemblage change in the North Atlantic Ocean responded directly to the onset of global warming during the last deglaciation. However, assemblages continued to change during the current warm period (i.e., Holocene) postdating the last deglaciation by several thousands of years even though the temperature forcing is comparably low during the Holocene. We observe a similar pattern among other (functional) plankton groups (Chapter 4). For planktonic foraminifera over half of the overall assemblage change (54 %) during the investigated time period of the past 24 thousand years (kyr) occurred during the current warm period (past 11.7 kyr), whereas only 34 % of the global mean sea surface temperature (SST) change during the same time period can be attributed to the current warm period (Figure 5-1). This finding is surprising, because SST is arguably the main predictor of planktonic foraminifera species composition (Morey et al., 2005; Rillo et al., 2021). As discussed in detail in Chapter 3 and 4, a potential explanation for this might be a shift in the dominant drivers of assemblage change from more abiotic causes (i.e., temperature forcing) during the last deglaciation to more biotic causes (i.e., species interactions) during the current warm period. However, questions remain about the exact influence of climate on the observed assemblage change during the Holocene.

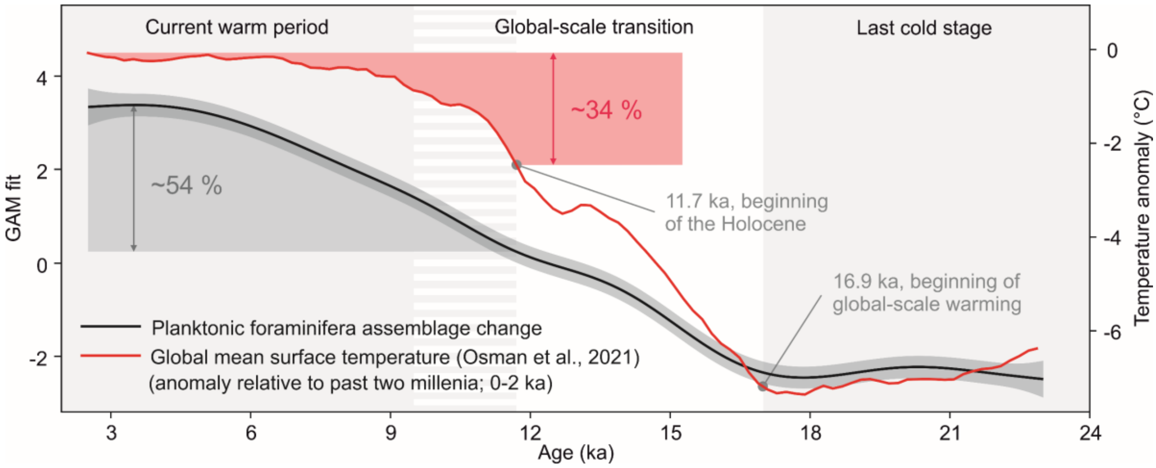


**Figure 5-1:** Overall planktonic foraminifera assemblage change for the North Atlantic Ocean and global mean sea surface temperature (Osman et al., 2021) for the past 24 kyr. Highlighted is the relative change that can be attributed to the current warm period (past 11.7 kyr; grey and red shading). Overall compositional change is shown as a generalised additive model (GAM) fit and its 95% confidence interval (dark grey shading) and based on 25 individual planktonic foraminifera assemblage time series (see Chapter 3 for more information). The temperature anomaly is referenced to the past two millennia (0-2 ka).

In this manuscript, we focus our analysis on two different aspects of the observed discrepancy between assemblage change and temperature change during the current warm period (Figure 5-1) using the same planktonic foraminifera assemblage composition time series as in our previous study. In our initial study (Chapter 3) we compared the overall planktonic foraminifera assemblage change in the North Atlantic Ocean to independent global mean SST change. However, the overall assemblage change in the North Atlantic is the result of assemblage change at the local scale, which reflects local, rather than global temperature. So, it is important to investigate whether our main finding also holds when looking at the local scale, i.e., when local assemblage change is compared to local temperature change. Because future warming is projected to vary spatially (IPCC, 2023), understanding how plankton has responded to environmental change on the local scale will be essential to improve predictions of how species communities will respond to the ongoing climate crisis. Since we observed the prolonged overall planktonic foraminifera assemblage change during the Holocene, we focus our analysis in the first part of this study on the past 11.7 kyr and investigate the relationship between local planktonic foraminifera assemblage change and independently reconstructed local temperature. Since the overall planktonic foraminifera assemblage change is a result of the local assemblage change and assemblages should respond more directly to the temperature change in their immediate local environment rather than global mean SST, we expect a smaller discrepancy between local assemblage change and local SST change. In the first part our analysis, we therefore test following hypothesis:

**H3.1: Local SST change explains more variance in planktonic foraminifera assemblage change during the Holocene than global SST**

The observed discrepancy between overall assemblage change and global mean SST change (Figure 5-1) may also indicate a possible change of the relationship between assemblage change and temperature change with the beginning of the Holocene. However, this would contradict the assumption of uniformitarianism, i.e., the drivers of community change have not changed over time, which is widely used in applied palaeoecological and paleoclimate research (e.g., Guiot and de Vernal, 2007) and biodiversity modelling to model community responses to past or future climate change (Guisan and Thuiller, 2005; Elith and Leathwick, 2009). Testing the assumption of uniformitarianism is difficult as the true temperature evolution of the Holocene can only be reconstructed using indirect means and may differ from the reconstructed temperature change.

However, given that SST is the main predictor of planktonic foraminifera species composition today (Morey et al., 2005; Rillo et al., 2021) and the assumption of uniformitarianism, i.e. that this relationship has not changed over time and therefore space-for-time substitution works, we can use planktonic foraminifera assemblages to calculate SST (hereinafter PF SST) to analyse how much variance of the assemblage change can in theory be explained by temperature change and compare it between time periods (Figure 5-2).

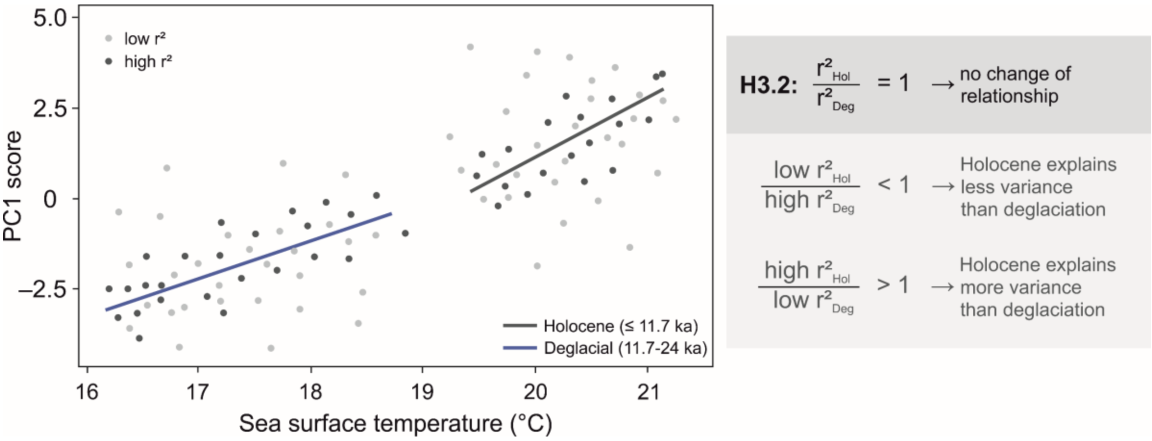


**Figure 5-2:** Comparing the relationship between assemblage change and planktonic foraminifera-derived sea surface temperature (PF SST) between the Holocene (past 11.7 kyr) and the last deglaciation and cold stage (11.7-24 kyr). Assemblage change is given as the first principal component score (PC1). Hypothesis H3.2 states that there is no difference in the relationship of planktonic foraminifera assemblages and PF SST during the past 24 kyr. For this, the variance in assemblage change that is explainable by PF SST during the Holocene is compared with the variance during the last deglaciation and cold stage. Two alternative examples of the potential influence of high and low $r^2$ values on the hypothesis are given.

So, in the second part of this manuscript we calculate the ratio of the variance of the planktonic foraminifera assemblage change that can be in theory explained by PF SST between the Holocene (past 11.7 kyr) compared to the last deglaciation and cold stage (11.7-24 kyr). If there is no change in the relationship between assemblage change and temperature change, we expect that the ratio of explained variances ($r^2_{Hol}/r^2_{Deg}$) during the past 11.7 kyr and during 11.7-24 kyr is 1 (Figure 5-2). A ratio deviating from 1 would indicate that the relationship between PF SST and assemblage change is less well constrained during the past 24 kyr. A ratio of less than 1 would indicate that the PF SST explains less of the variance in the Holocene than in the glacial assemblages and a ratio of greater than 1 would indicate that the PF SST explains more of the variance in the Holocene than in the glacial assemblages (Figure 5-2). Assuming that uniformitarianism holds, we test following hypothesis in the second part of this our analysis:

**H3.2: There is no difference between the relationship of planktonic foraminifera assemblages and PF SST in the current warm period compared to the last deglaciation and cold stage**

## 5.2 Material and approach

### 5.2.1 Planktonic foraminifera assemblage data

The data analysis is based on the same 25 planktonic foraminifera assemblage time series from the North Atlantic Ocean that we used before (Figure 5-3; Chapter 3.4.1). All time series cover the full latitudinal range of the basin (i.e., 72°N to 6°S; Figure 5-3) and the entire time period of interest (i.e., beginning at least 23 ka and ranging to at least 2.5 ka) with an average resolution of 600 years, ranging from 40 to 1300 years (see Extended Data Table 1 of Chapter 3). 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. For the 9 sites that are included in the PALMOD 130k marine palaeoclimate data synthesis V1.1 (Jonkers et al., 2020), we used their provided revised age models and for the 16 sites not included in the synthesis we used the same approach as in Jonkers et al. (2020). For further information on the data selection process, age model revision and harmonisation of planktonic foraminifera taxonomy please see Chapter 3.4.1 and 4.2.1.

We applied principal component analysis (PCA) on the standardised planktonic foraminifera assemblage data and extracted, for each time series, the first principal component (PC1). Since the PC1 explains most variance in the assemblage data, we can use it as a measure of local assemblage change. To align all PC1 axes in the same direction, we checked and, if necessary, changed their sign by fitting linear models through all PC1 scores vs age. To adjust for the different temporal resolution of the individual time series, we binned all data into 500-year bins and calculated the average mean PC1 score of each bin per time series. Time bins without data remained empty.

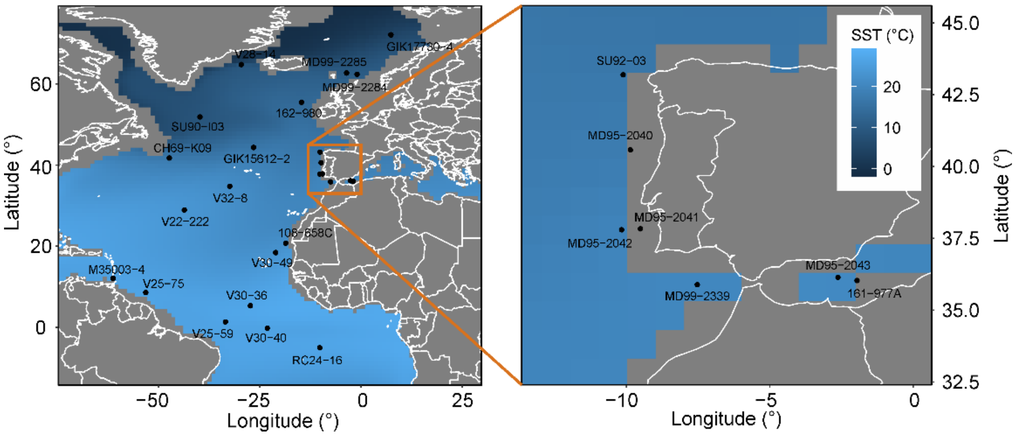


**Figure 5-3:** Location of the 25 planktonic foraminifera assemblage time series (black dots). Left: Overview map with marked location of the zoom-in (orange rectangle), right: Zoom-in to Iberian Peninsula. Background: Sea surface temperature (SST) at 0.1 ka from Last Glacial Maximum reanalysis (Osman et al., 2021). Grid cells at which the LGMR contains no data are filled in dark grey.

### 5.2.2 Independent local sea surface temperature reconstructions

In the first part of our analysis, we use independent local mean annual SST from the Last Glacial Maximum reanalysis (LGMR; Osman et al., 2021) to test our first hypothesis (H3.1). The LGMR is a proxy-constrained reanalysis of global climate parameters (including SST) for the past 24 kyr at a resolution of 200 years and combines 539 proxy records with independent model information from the Community Earth System Model (Osman et al., 2021). At each location of the 25 planktonic foraminifera assemblage time series, we extracted mean annual SST time series from the corresponding grid cell of the LGMR grid. For the three sites (161-977A, MD95-2040 and MD95-2041; Figure 5-3b) at which location no data is available, sea surface temperature data from the nearest grid cell was extracted. We binned the local LGMR SST into the same 500-year bins as the assemblage data and calculated the average mean annual SST of each bin per reconstruction. For the alignment of the local SST reconstructions (hereinafter local LGMR SST) with the planktonic foraminifera assemblage data, we ignored chronological uncertainties beyond the binning approach.

### 5.2.3 Planktonic foraminifera sea surface temperature

To address the second hypothesis (H3.2), we calculate PF SST. Since SST is the main predictor of modern planktonic foraminifera species composition (Morey et al., 2005; Rillo et al., 2021), we can translate this spatial relationship onto the temporal scale (space-for-time substitution) and predict planktonic foraminifera-derived SST. By doing so we assume that (1) SST is the main cause of change in planktonic foraminifera assemblages (stationarity principle), (2) the relationship between planktonic foraminifera and SST has not changed over time (uniformitarianism), and (3) the modern calibration dataset contains all the information needed to interpret the fossil assemblage data (Guiot and de Vernal, 2007).

We used two different approaches to calculate PF SST: The Modern Analogue Technique (MAT) and the Weighted Averaging Partial Least Squares (WA-PLS) approach. The MAT approach (Hutson, 1980; also known as k-nearest neighbour) is based on the comparison of fossil assemblages and a modern calibration dataset to identify a set of modern analogues that are most similar to the fossil sample. Dissimilarities between modern and fossil assemblages were calculated using the squared chord distance, which has been shown to effectively identify analogues in microfossil datasets (Prell, 1985). The WA-PLS regression approach (ter Braak and Juggins, 1993) assumes that species assemblages can be expressed as a function of their predicting variable. The direct relationship between modern SST and the modern assemblages is calculated and then used to translate fossil assemblages into past SST. The performance of both approaches was tested by internal bootstrap cross-validation with 1000 repetitions. The optimal number of analogues (MAT) and components (WA-PLS), on which the SST reconstructions are based, were estimated using the best combination of low root mean squared error of prediction (RMSEP), low maximal bias and high r² values. Since cross-validation yielded similar results for different number of analogues (respective components), we also checked the percentage reduction of RMSEP per analogue (respective component) to choose the most parsimonious solution and prevent over-fitting (Juggins and Birks, 2012). For MAT SST reconstruction we use the weighted average of the three most similar samples and for WA-PLS reconstructions we use four components (Table 5-1).

**Table 5-1:** Performance of Modern Analogue Technique (MAT) and Weighted Averaging Partial Least Square (WA-PLS) in relation to the number of analogues (respective components). Both approaches were tested by internal bootstrap cross-validation with 1000 repetitions. The optimal number of analogues (respective components) are highlighted and represent the best combination of low root mean squared error of prediction (RMSEP), the percentage change in RMSEP, low maximal bias and the variance explained (r²).

| MAT | | | | | WA-PLS | | | | |
|---|---|---|---|---|---|---|---|---|---|
| k | RMSEP (°C) | % change in RMSEP | Max. bias (°C) | r² | c | RMSEP (°C) | % change in RMSEP | Max. bias (°C) | r² |
| 1 | 1.063 | - | 0.503 | 0.9890 | 1 | 2.051 | - | 2.527 | 0.9353 |
| 2 | 0.992 | 6.70 | 0.485 | 0.9897 | 2 | 1.757 | 14.32 | 1.520 | 0.9525 |
| **3** | **0.955** | **3.70** | **0.519** | **0.9900** | 3 | 1.696 | 3.51 | 1.415 | 0.9560 |
| 4 | 0.937 | 1.85 | 0.553 | 0.9899 | **4** | **1.621** | **4.38** | **1.296** | **0.9603** |
| 5 | 0.929 | 0.88 | 0.580 | 0.9898 | 5 | 1.590 | 1.91 | 1.356 | 0.9617 |

For the modern calibration dataset, we used the North Atlantic Ocean regional subset of the ForCenS database (Siccha and Kucera, 2017). We justify the use of this regional subset even though two time series of this analysis fall within the Mediterranean Sea (western Alboran Sea) and two time series are situated in the equatorial South Atlantic Ocean (Figure 5-3), because all samples have a strong North Atlantic influence. For sites in the calibration dataset with replicated counts, single randomly chosen samples were preserved, resulting in 1259 individual sites. For each site in the calibration dataset, annual SST data from 50 m water depth from the World Ocean Atlas 1998 (Levitus and US National Oceanographic Data Center, 2012) was derived from a 100 km-radius buffer around each location, because sediment samples integrate the export flux of planktonic foraminifera over a larger area above the core site (v. Gyldenfeldt et al., 2000; van Sebille et al., 2015).

### 5.2.4 R packages

All statistical analyses (described in the corresponding parts 1 and 2) were performed in R version 4.1.3 (R Core Team, 2024) using the ‘tidyverse’ packages (Wickham et al., 2019) and the ‘janitor’ package (Firke, 2023) for cleaning and importing the data; ‘Hmisc’ (Harrel Jr, 2021) for data binning; ‘FactoMineR’ (Lê et al., 2008) and ‘factoextra’ (Kassambara and Mundt, 2020) for PCA; ‘vegan’ (Oksanen et al., 2020) for DCA; ‘rioja’ (Juggins, 2020) for MAT and WA-PLS; ‘ncdf4’ (Pierce, 2023) and ‘FNN’ (Beygelzimer et al., 2023) for extraction of LGMR SST and ‘ggplot2’ (Wickham, 2016) for the plots.

## 5.3 Part 1: Local Holocene planktonic foraminifera assemblage change

We used linear regression models to compare the relationship of planktonic foraminifera assemblage change with independent local LGMR SST change in the Holocene. We observe a significant linear relationship ($p \leq 0.05$) between planktonic foraminifera assemblage change (PC1) and local LGMR SST in 11 out of the 25 sites, with most sites displaying a positive relationship. In 1 out of the 11 significant sites we observe a negative relationship between SST and assemblage change (Figure 5-4a). In contrast, when compared to the global LGMR SST, planktonic foraminifera assemblage change shows a significant linear relationship with SST in 19 out of the 25 sites (Figure 5-4b). The median $r^2$ value for the analysis using local LGMR SST is 0.26, while the median $r^2$ value for the analysis using global LGMR SST is 0.51 (Figure 5-4c), indicating no improvement of the observed Holocene discrepancy between planktonic foraminifera assemblage change and SST change when using local comparisons. We tested the significance of the differences between the median values using the two-sample Wilcoxon signed rank test with the null hypothesis that the median of the paired variance differences between the two groups is zero (i.e., there is no significant difference between the amount of variance explained by the local and global LGMR SST reconstruction). There is sufficient evidence ($p = 0.005$) for the rejection of the null hypothesis H3.1 meaning that global LGMR SST explains more of the variance in the planktonic foraminifera assemblage change than local LGMR SST.

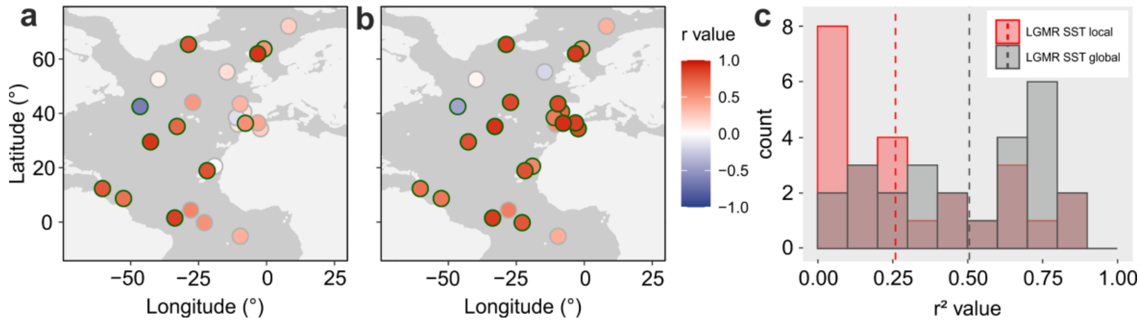


**Figure 5-4:** Spatial pattern of correlation between planktonic foraminifera assemblages (PC1) and Last Glacial Maximum reanalysis (LGMR) sea surface temperature (SST) during the current warm period (past 11.7 kyr). (a) Correlation coefficient r of PC1 versus local LGMR SST; (b) Correlation coefficient r of PC1 versus global LGMR SST and (c) histogram of variance in PC1 that is explained by local and global LGMR SST. Locations with a significant linear relationship ($p <= 0.05$) are highlighted by green circle outlines (a,b) and median values are given as dashed vertical lines (c).

The comparison between the relationship of planktonic foraminifera assemblage change with local and global LGMR SST change during the Holocene revealed intriguing disparities, prompting further investigation into the spatial pattern of total change during the past 24 kyr. For this, we calculated how much of the total change that we observed during the past 24 kyr occurred in the Holocene and found that the spatial pattern in the local LGMR SST is at odds with the spatial pattern in the planktonic foraminifera change (Figure 5-5). On average, about 57 % of the local planktonic foraminifera assemblages change and only about 30 % of the local temperature change of the past 24 kyr occurred during the current warm period. The Holocene assemblage change ranges locally from 24-100 % and increases with latitude (Figure 5-5a,c). In contrast, the local LGMR SST shows a negative trend. Here, the Holocene temperature change decreases with latitude and locally ranges from 16-47 % (Figure 5-5b,d), with the highest values occurring at the equatorial sites.

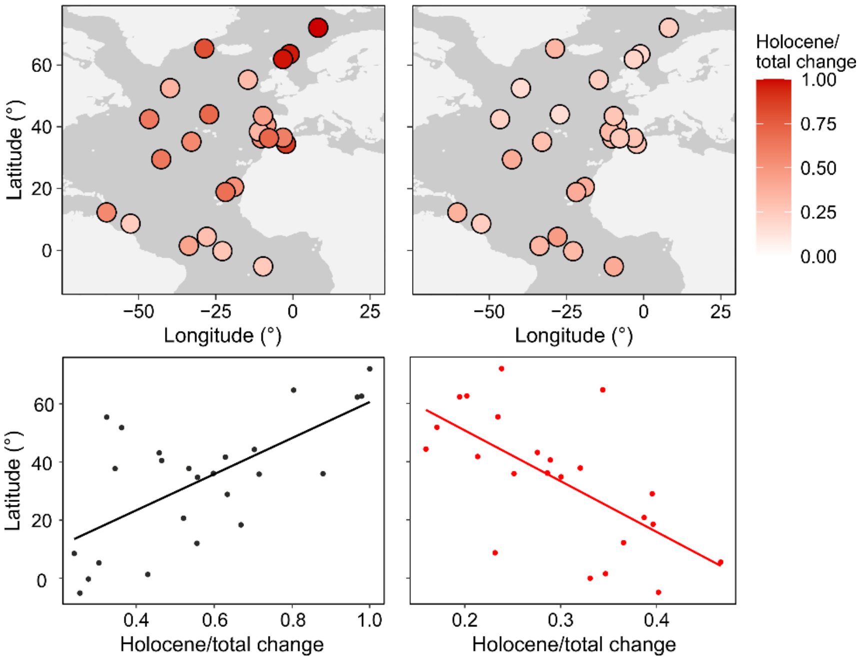


**Figure 5-5:** Spatial pattern of the amount of (a) planktonic foraminifera assemblage change and (b) local Last Glacial Maximum reanalysis (LGMR) sea surface temperature (SST) change that happened in the Holocene (past 11.7 kyr) compared to the past 24 kyr. (c,d) Relationship between latitude and Holocene change for (c) planktonic foraminifera assemblages and (d) LGMR SST.

We estimated the rate of Holocene change for planktonic foraminifera assemblage change and local LGMR SST using the slope of linear regression models. We observe local planktonic foraminifera assemblage change at almost all sites (Figure 5-6a), while local LGMR SST shows no change or only very slight increases during the past 11.7 kyr (Figure 5-6b). On average, Holocene LGMR SST change is 0.06 °C per kyr, resulting in an average temperature increase of 0.76 °C during the current warm period (past 11.7 kyr). No clear spatial pattern in the rate of local assemblage and temperature change during the current warm period can be observed.

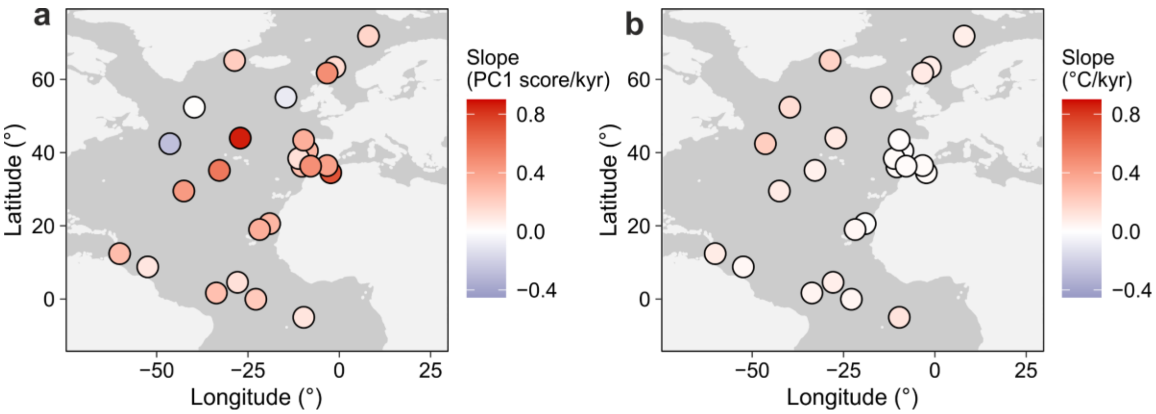


**Figure 5-6:** Rate of local Holocene change in (a) planktonic foraminifera assemblages and (b) LGMR SST in the North Atlantic Ocean given as the slopes of linear regression models.

Contrary to our first hypothesis (H1) that local SST explains more variance in planktonic foraminifera assemblage change during the current warm period than global mean SST, we observe a different pattern. In fact, global LGMR SST explains more variance in local planktonic foraminifera assemblage change than local LGMR SST (Figure 5-4), resulting in no improvement when using local LGMR SST. This observation is puzzling, expecting that assemblages respond to temperature changes in their local environment rather than global SST. Additionally, the Holocene spatial pattern in the local LGMR SST change is at odds with the Holocene spatial pattern in the planktonic foraminifera change. We observe more change in assemblages than in local LGMR SST (Figure 5-5 and Figure 5-6) and a different latitudinal pattern in the partitioning of change since the last cold stage, with Holocene assemblage change increasing with latitude, while Holocene temperature change decreases with latitude (Figure 5-5c,d). This is contrary to our expectation, because we would expect the assemblage change to be positively correlated with local LGMR SST given that SST is the main predictor of planktonic foraminifera species composition (Morey et al., 2005; Rillo et al., 2021). We can reasonably rule out effects of age uncertainty, temporal resolution, spatial homogenisation and ecological and environmental factors.

In this study, we revised all age models using the same approach as in Jonkers et al. (2020), however, we did not account for specific age uncertainties in the age models beyond the binning approach. So, the possible misalignment of the assemblage data with LGMR SST and therefore a lack of synchronisation could introduce lagged responses of the planktonic foraminifera assemblages and weaken the correlation between the assemblage change and LGMR SST leading a lower explanatory power. Since the LGMR SST shows no or only a very low increase in SST during the current warm period (Figure 5-6b), we would expect no significant change in the explained variance when accounting for age uncertainties. Moreover, age uncertainties in the assemblage data affect the overall explanatory power of LGMR SST regardless of whether the local or global reconstructions are used and, therefore, cannot explain the discrepancy between the predictive power of local LGMR SST compared to global LGMR SST. Since both SST reconstructions are derived from the same reanalysis and have the same temporal resolution of 200 years (Osman et al., 2021), we can also exclude the temporal resolution of the SST reconstructions as a potential cause for this discrepancy.

It is known that global climate models tend to spatially homogenize data. Global climate models are designed to simulate the Earth's climate on a global scale and, due to computational limitations, must parameterize complex processes of the climate system, and these parameterizations may not fully reflect all physical properties, especially at the local scale. Furthermore, global climate models are rather coarse in their spatial resolution (here a nominal resolution of 1° with enhancements near the equator and in the North Atlantic Ocean; Brady et al., 2019), which leads to a smoothing of fine-scale changes. However, this could only explain why local and global LGMR SSTs give the same results, not that the local LGMR SST is worse.

Even though SST is assumed to be the main predictor of planktonic foraminifera assemblage change (Morey et al., 2005; Rillo et al., 2021), ecological interactions (Lima-Mendez et al., 2015) and other environmental factors (Rillo et al., 2021) might increase in importance and also vary locally especially during times where overall temperature change is relatively low (i.e., the Holocene). Indeed, these different factors might be an explanation for the overall discrepancies between planktonic foraminifera assemblage change and SST change during the Holocene, but it is no explanation for the differences between both LGMR SST reconstructions.

The fact that the spatial variance in the local LGMR SST is at odds with the variance in the assemblages (Figure 5-5 and Figure 5-6) might be an indication that local SST reconstructions from global climate models need to be applied and interpreted with caution as they might not reflect realistic local SST variations especially in times with relatively low overall temperature change (i.e., the Holocene). So, even though the difference between the variance in the planktonic foraminifera assemblage change and the local and global LGMR SSTs during the Holocene is statistically significant ($p = 0.005$), we wonder to what extent it could be a coincidence or a reflection of the location of the sites.

There is insufficient evidence to accept the third hypothesis (H1: More variance in planktonic foraminifera assemblage change during the Holocene is explained by SST using local comparisons compared to the global comparison). Our observed counterintuitive results (Figure 5-4, Figure 5-5 and Figure 5-6) amplify the need for critical evaluation of SST reconstructions, especially when used to predict compositional turnover changes or test ecological assumptions/concepts (e.g., Blois et al., 2013; Antell et al., 2021; Fenton et al., 2023). These studies provide valuable and plausible information, assuming that SST reconstructions from model simulations reflect true environmental changes. For example, findings such as the stability of the thermal niches of planktonic foraminifera over the past 700 kyr (Antell et al., 2021) or the justification of space-for-time substitutions to model species responses to climate change (Blois et al., 2013) are conditional on the assumption that the simulated temperature accurately reflects the temperature that shaped the assemblages. Proxy-constrained reanalyses of SST reconstructions from climate model simulations, such as the one used in this study, can help refine predictions, but should still be critically evaluated as shown by our counterintuitive results. Since a comparison of climate model simulations with observational data is not possible in the past, validation of climate model outputs relies on the comparison with proxy reconstructions. Comparing the model with a multi-proxy approach might help to identify potential biases and uncertainties in the models and circumvent the problem that some proxies may also carry a non-climatic signal, providing insight into the ability of the simulation to reproduce observed climate patterns.

## 5.4 Part 2: Analysing the relationship between assemblage change and planktonic foraminifera sea surface temperature

Given the uncertainty about the reanalysis (i.e., LGMR SST), we investigate how much of the assemblage change could in theory reflect temperature change. We do this using the principle of uniformitarianism and the established SST-assemblage relationship. The principle of uniformitarianism in palaeoceanography states the relationship between planktonic foraminifera and SST today has not changed over time. In this context, it means that the relationship between planktonic foraminifera assemblages and SST observed today can be used as a guide to understand how these assemblages might have responded to past changes in SST. If the present relationship between foraminifera assemblages and SST holds true over time, then we can use it as a proxy to estimate past SST based on the observed assemblage changes. By employing analogue and transfer function approaches, we calculated PF SST, allowing us to estimate how much of the observed assemblage change could theoretically be attributed to temperature change.

### 5.4.1 Holocene planktonic foraminifera sea surface temperature

We demonstrate that transfer functions and analogue techniques work in space, by directly comparing the planktonic foraminifera assemblages in the regional ForCenS dataset to the observed modern temperatures. For this, we conducted a detrended correspondence analysis and extracted the first detrended correspondence axis (DCA1), because planktonic foraminifera species have unimodal temperature distributions (i.e., an optimum where the species performs best).

We observe a strong relationship ($r^2 = 0.95$) between planktonic foraminifera assemblages of the regional ForCenS calibration dataset and PF SST (Figure 5-7a). Modern SST explains almost all of the variance in the DCA1 scores of the planktonic foraminifera assemblages, confirming that species assemblage composition is tightly linked to temperature. We use the MAT and WA-PLS approaches to calculate planktonic foraminifera-derived SST and test their performance against the calibration dataset. The performance of both reconstruction approaches is very good ($r^2_{MAT} = 0.99$ and $r^2_{WA\text{-}PLS} = 0.96$) with only minor differences (Figure 5-7b,c). The WA-PLS approach systematically underestimates SST between 6-1°C and overestimates SST below 1°C as WA-PLS does not generate reconstructions colder than 1 °C (Figure 5-7c).

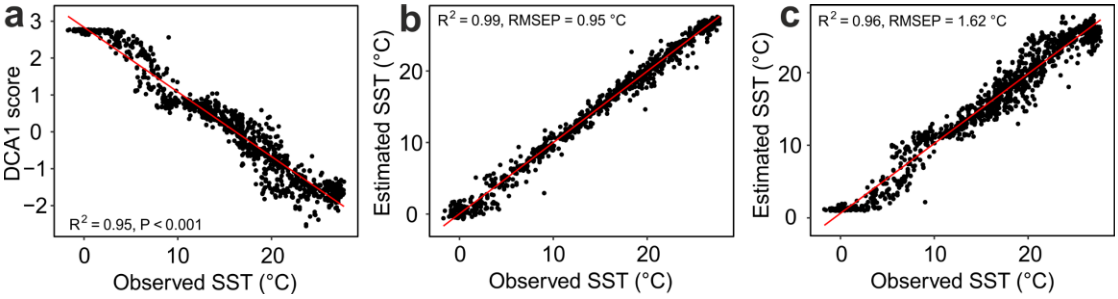


**Figure 5-7:** Performance of planktonic foraminifera-derived temperature calibrations. (a) Scores of first Detrended Component Analysis axis (DCA1) versus observed modern sea surface temperature (SST); (b) estimated Modern Analogue Technique (MAT) SST versus observed modern SST using the three nearest analogues and (c) and estimated Weighted-Averages - Partial Least Square (WA-PLS) SST versus observed modern SST using four components. The performance of both methods was tested by internal bootstrap cross-validation with 1000 repetitions.

We used linear regression models to compare the relationship of planktonic foraminifera assemblage change with PF SST change in the Holocene. We observe a significant linear relation ($p \leq 0.05$) between planktonic foraminifera assemblage change and MAT and WA-PLS SST in 16 and 20 sites in the North Atlantic Ocean during the current warm period (Figure 5-8a,b). All of the sites with a significant linear relationship show a positive relationship with MAT and WA-PLS SST and correlation between planktonic foraminifera assemblage change and MAT and WA-PLS among individual sites are comparable (Figure 5-8c). There is sufficient evidence (*p* = 0.007) that the median $r^2$ values of MAT and WA-PLS SST are significantly different, meaning that WA-PLS SST explains more variance in the planktonic foraminifera assemblage data than MAT SST. The median $r^2$ value for the analysis using MAT SST is 0.53 and for WA-PLS SST 0.69 (Figure 5-8d), more than twice as large as that explained by the local LGMR SST ($r^2$ = 0.26) and in the range of global LGMR SST ($r^2$ = 0.51; Figure 5-4c).

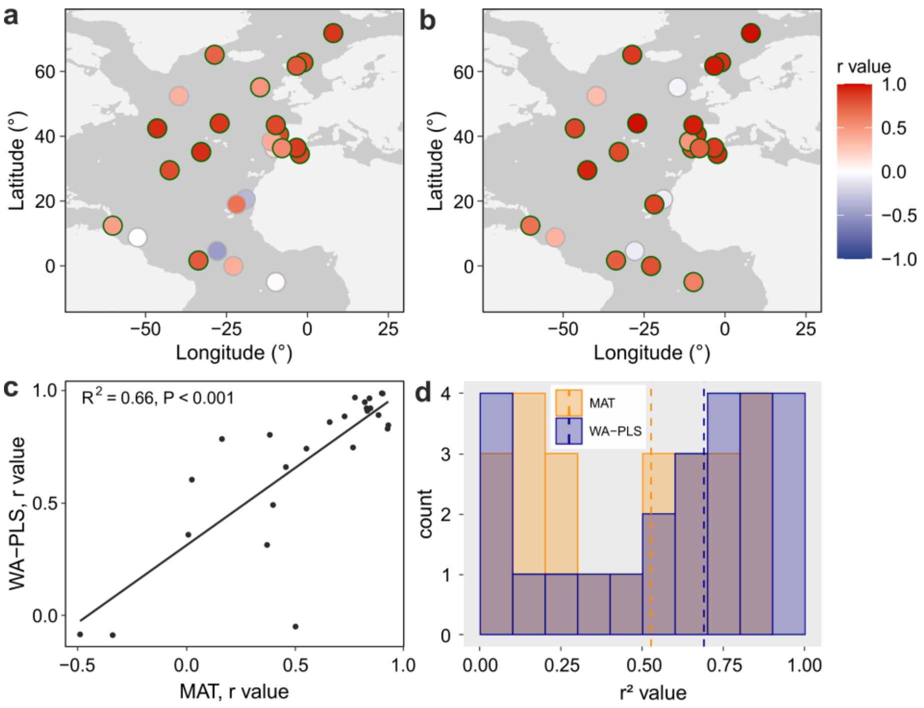


**Figure 5-8:** Spatial pattern of correlation between planktonic foraminifera assemblages (PC1) and Modern Analogue Technique (MAT) and Weighted-Averages - Partial Least Square (WA-PLS) sea surface temperature (SST) during the current warm period (past 11.7 kyr). (a) Correlation coefficient r of PC1 versus MAT SST; (b) correlation coefficient r of PC1 versus WA-PLS SST; and (c)their relationship. (d) Histogram of variance in PC1 that is explained by MAT and WA-PLS SST. Locations with a significant linear relation ($p <= 0.05$) are highlighted by green circle outlines (a,b) and median values are given as dashed vertical lines (d).

Overall, the PF SSTs (MAT and WA-PLS) show more Holocene change than the local LGMR SST (Figure 5-9a,b). On average, MAT SST increases by 0.14 °C per kyr and WA-PLS by 0.19 °C per kyr, resulting in an average temperature increase of 1.64 °C and 2.25 °C, respectively, during the current warm period, which is two to three times higher than the increase in local LGMR SST. Like in the local LGMR SST, no clear spatial pattern of Holocene temperature change is observed in the PF SSTs. However, based on the spatial calibration of planktonic foraminifera assemblages, we show that the Holocene assemblage change could be associated with more temperature change than shown by LGMR SST (Figure 5-6b and Figure 5-9).

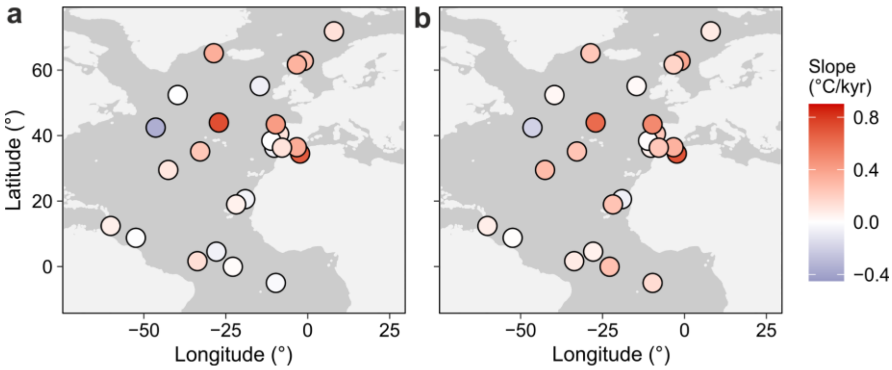


**Figure 5-9:** Rate of Holocene change planktonic foraminifera-derived sea surface temperature (SST) changes in the North Atlantic Ocean during the current warm period. (a) Modern Analogue Technique (MAT) SST and (b) Weighted-Averages - Partial Least Square (WA-PLS) SST given as slopes of linear regression models.

### 5.4.2 Analysing the relationship between assemblage change and planktonic foraminifera sea surface temperature

After confirming our initial conclusion that not all of the observed local assemblage change in the Holocene can be explained by SST alone (Chapter 3) through the analysis of planktonic foraminifera-derived SST (Figure 5-8), we now investigate whether there has been a change in the relationship between planktonic foraminifera assemblages and PF SST during the past 24 kyr. For this, we calculated the variance ratio between the current warm period (i.e., the past 11.7 kyr) and the last deglaciation and cold stage (i.e., 11.7-24 kyr) (Figure 5-10). Assuming that SST is the main predictor of planktonic foraminifera assemblage change over time and that this relationship has not changed, we would expect these ratios to be 1, as there should be no difference between the current warm period and the last deglaciation and cold stage (Figure 5-2).

We observe a large spread in the variance ratios and the median of the variance ratios is below 1 (0.86 for both MAT and WA-PLS), indicating that less variance in faunal change can be explained by temperature in the Holocene compared to the last deglaciation and cold stage (Figure 5-10). We tested if the median of the variance ratios ($r^2_{\mathrm{Hol}}/r^2_{\mathrm{Deg}}$) is different from 1 (i.e., less than 1) using the one-sample Wilcoxon signed rank test with the null hypothesis that the median of the variance ratio is greater than or equal to 1. However, the deviation of the variance ratio from 1 is not significant for either WA-PLS SST ($p$ = 0.074) or MAT SST ($p$ = 0.289), so there is insufficient evidence to reject the null hypotheses. This leads to the acceptance of our second hypothesis H3.2, that there is no significant difference between the relationship between planktonic foraminifera assemblages and PF SST in the current warm period compared to the last deglaciation and cold stage.

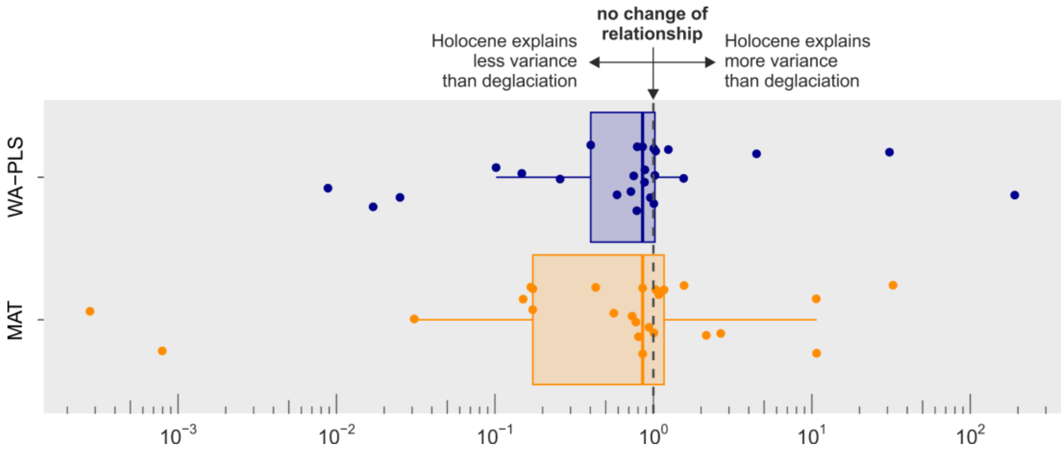


**Figure 5-10:** Comparison of the relationship between changes in planktonic foraminifera assemblages and changes in planktonic foraminifera-derived sea surface temperature (PF SST) during the current warm period (past 11.7 kyr) and the last deglaciation and cold stage (11.7-24 kyr). Ratio between the variance in faunal change ($r^2_{Hol}/r^2_{Deg}$) that can in theory be explained by SST in the current warm period compared to the deglaciation. The lower and upper hinges of the box plots correspond to the 25th and 75th percentiles, and the median is indicated by the bold vertical lines. The lower and upper whiskers are constrained within the 1.5*IQR (interquartile range). The dashed vertical line indicates 1 (the null hypothesis). The variance ratios are plotted on a logarithmic scale.

The observations made in this study, strengthen our initial finding (Chapter 3) that a considerable amount of the observed planktonic foraminifera compositional change in the North Atlantic Ocean during the current warm period cannot be explained by SST alone. This conclusion holds true at both the global and local scales, when comparing assemblage changes with the LGMR SSTs. We further show that the prolonged planktonic foraminifera assemblage change in the Holocene was not caused by a change in the relationship between SST and planktonic foraminifera assemblage change (acceptance of hypothesis H3.2) during the past 24 kyr, which is in accordance with the findings of Antell et al. (2021) that the thermal niches of planktonic foraminifera have not changed during the past 700 kyr. Instead, it may indicate that during the Holocene, when overall temperature change was relatively low, factors other than temperature change played a more important role in the shaping of the planktonic foraminifera assemblages. Recent evidence from terrestrial studies (Doncaster et al., 2023) further supports the idea that assemblage change during the Holocene is not solely driven by environmental change. They observed a shift in the dominant drivers of terrestrial plant assemblage change from environmental forcing being the main driver of assemblage change until about 9 ka ago, to internal processes (e.g., ecological interactions) becoming more important thereafter.

Considering this, caution must be exercised in time-for-space substitutions, especially during times with small temperature change. This is evident at certain sites in the North Atlantic Ocean, where PF SST explains only a small portion of the variance in planktonic foraminifera assemblage change during the Holocene (Figure 5-8a,b). It has been shown that environmental parameters alone are not sufficient enough to predict the community structure of marine plankton (Lima-Mendez et al., 2015) and that other environmental factors such as insolation, water column stratification, salinity, and nutrient availability (Solignac et al., 2006; Rillo et al., 2021) may play a role in marine plankton dynamics, and their local variability may be particularly relevant during periods of relatively small overall temperature change, such as the Holocene. Furthermore, although planktonic foraminifera-derived SST showed a strong correlation with modern assemblage composition ($r^2 = 0.95$; Figure 5-7a), its effectiveness in explaining assemblage change over small temperature ranges remains uncertain due to the large range of modern SST covered by the calibration dataset. Consequently, reliance on SST alone as a predictor of planktonic foraminifera community dynamics may be subject to inaccuracies and should be approached with caution in such contexts.

## 5.5 Conclusion

The aim of this study was to address the discrepancy between overall planktonic foraminifera change and global SST observed in the North Atlantic Ocean during the current warm period, as identified in Chapter 3. By investigating the response of local planktonic foraminifera assemblage change to local SST during the current warm period, and by analysing the relationship between planktonic foraminifera assemblage change and PF SST during the past 24 kyr, our results shed further light on the mechanisms driving this discrepancy. Based on our analysis, the following conclusions can be drawn:

(1) The spatial variance in the local LGMR SST reconstruction inconsistent with the variance in the planktonic foraminifera assemblages, suggesting that the local LGMR SST reconstruction may underestimate the true local SST changes during the Holocene.

(2) A considerable amount of the observed planktonic foraminifera assemblage change in the North Atlantic Ocean during the current warm period cannot be explained by SST alone. However, there is no evidence that the relationship between planktonic foraminifera assemblages and SST has changed at the local scale since the transition from the last cold stage to the current warm period.

Our study highlights that data analyses that are based on SST reconstructions (including modelled SST) must always be interpreted with caution, and the limitations and uncertainties of the specific SST approaches must be accounted for. For example, local SST from global climate models generally suffer from spatial homogenization and in this study, local LGMR SST performed worse than planktonic foraminifera-derived SST, which in turn lacks independence. We therefore suggest a critical evaluation of SST reconstructions (e.g., by combining independent multiproxy and model reconstructions) before using them to predict species composition or to test ecological concepts. The results of such analyses are valuable for a comprehensive understanding of planktonic foraminifera responses to climate change, but also depend on the assumption that the simulated or reconstructed SST accurately reflects the true SST.

# 6 Manuscript IV

## How to improve the reusability of micropalaeontological assemblage data? (or: Who knows *Globorotalia mentum*?) - A planktonic foraminifera case study

**T. Strack, L. Jonkers, R. Huber, and M. Kucera**
Manuscript in preparation for submission

### Abstract

The sedimentary record of marine microfossil assemblages provides valuable insights into long-term biodiversity shifts, a perspective not attainable through short-term observational data. Open data sharing through dedicated repositories has facilitated data synthesis and climate change research. However, data harmonisation remains challenging due to complex semantics, inconsistent taxonomic practices, and ever-evolving taxonomic concepts. This study presents common challenges associated with legacy count data of planktonic foraminifera, a vital marine plankton group for studying past climate and biogeography changes, highlighting the need for comprehensive community-defined (meta)data standards to enhance data interoperability and reusability of marine microfossil assemblage data. Additionally, we propose an automated solution for harmonising count data of extant planktonic foraminifera publicly available on PANGAEA and provide examples of an ideal dataset.

### 6.1 Introduction

The sedimentary record of marine microfossil species assemblages offers the unique opportunity to observe long-term changes in biogeography and biodiversity and, indirectly, of past climate (Yasuhara et al., 2017), which are not observable in short-term observational data that rarely span more than 100 years (Dornelas et al., 2018). Large amounts of marine microfossil assemblage data have been collected over decades. Thanks to collaborative efforts that dates back to the 1970s and 1980s (CLIMAP Project Members, 1976, 1981), these datasets have to some degree been synthesised and used to study the long-term response of marine plankton to past climate change which can then help to evaluate the magnitude and impact predicted future climate change will have on the marine realm. Such synthesis efforts have only been possible because of the open sharing of data among micropalaeontologists that has since the turn of the millennium been facilitated by dedicated repositories such as PANGAEA (Felden et al., 2023) and NOAA's World Data Service for Paleoclimatology.

Over the last decade, there has been a huge and ongoing effort to make scientific data FAIR (Findable, Accessible, Interoperable, Reusable) and more transparent by using guiding principles and best practices (Wilkinson et al., 2016). The goal of the FAIR data principle is to make scientific data easier for machines and users to find, use and share. Finable data should be assigned globally unique and persistent identifiers, described with rich metadata and indexed in searchable resources such as publicly available data archives. Accessible data should be openly retrievable using standardised protocols without any restrictions or with minimal barriers such as embargo periods. Interoperable data should be presented in an applicable and accessible way and use vocabularies that follow the FAIR principles allowing for easy combination of datasets. Lastly, Reusable data should be well-documented and include sufficient information that is needed to reuse the data for different purposes.

Because of the long history of synthesis efforts and open approach to science of the micropalaeontological community, large amounts of microfossil data are already archived in publicly available data repositories. Even though an unknown, but likely minor, part of the data remains inaccessible, microfossil assemblage data is often findable and accessible. However, the interoperability as well as reusability of such data for global application is often hindered due to their complex semantics, reflecting the intricacies of biological nomenclature and its inconsistent application by users. There are different taxonomic schools which may use different classification criteria for specimens that can lead to discrepancies between datasets. Also, new taxonomic insights lead to the constant evolution of taxonomic concepts which then might result in the renaming of species and the recognition or dismissal of taxonomic synonyms. The constant revisions of taxonomic concepts and their inconsistent application by users lead to many studies that refer to the same taxa by using different names. This poses particular challenges when attempting to harmonise data that have been collected at different points in time. Moreover, micropalaeontological data are often collected in isolation and made publicly available as independent datasets with the purpose of the reproduction of individual studies rather than to facilitate reuse on a bigger scale (i.e., without a broader context or connection to other datasets). Also, incomplete documentation of (meta)data and the original study purpose might introduce potential biases into data syntheses and influence data interpretation. It further needs to be mentioned that datasets can only be compared and harmonised to the level of the data with the coarsest taxonomic resolution. Taxonomic data harmonisation to the highest possible resolution should always be aspired, as it might give us a better understanding of biodiversity. Together, these factors render the comparison and synthesis of micropalaeontological data cumbersome.

This complexity of taxonomic data harmonisation can be exemplified by sedimentary assemblage data of planktonic foraminifera - a group of calcifying marine zooplankton with global distribution. Even though planktonic foraminifera represent a small part of the diversity of marine organisms, they show diversity patterns that are comparable to other plankton, making them ideal organisms to study biogeographic patterns and the relationship of biodiversity change to past climate (Ezard et al., 2011; Yasuhara et al., 2012b; Fenton et al., 2016a; Yasuhara et al., 2020b). Planktonic foraminifera have an exhaustive and intensively studied fossil record and the available data already exceeds the threshold for manual curation (Siccha and Kucera, 2017). There is a long history of planktonic foraminifera data syntheses starting with the CLIMAP project in the 70s and 80s that aimed to map the climate state during the Last Glacial Maximum (CLIMAP Project Members, 1976, 1981). Since then, many syntheses such as Neptune (Lazarus, 1994; Renaudie et al., 2020), MARGO (Kucera et al., 2005a), ForCenS (Siccha and Kucera, 2017) and the recently published TRITON database (Fenton et al., 2021) have followed. These curated and globally consistent databases have for instance been used to show how the diversity gradient of planktonic foraminifera has developed over the past 40 million years (Fenton et al., 2023), how species richness of planktonic foraminifera has changed over the last 15 million years (Woodhouse et al., 2023), how planktonic foraminifera responded to long-term climate change in the North Atlantic Ocean during the past 24,000 years (Chapter 3), how modern planktonic foraminifera assemblages departed from their pre-industrial state (Jonkers et al., 2019) and how tropical planktonic foraminifera diversity may decline under future global warming (Yasuhara et al., 2020b). To unlock the full potential of microfossil data, we first need to understand the specific challenges that occur within individual taxonomic groups to improve the interoperability and reusability of microfossil data across many groups.

How to increase the reusability of micropalaeontological assemblage data highly depends on the data itself. For archived data (hereinafter legacy data) already in the public domain, tools that simplify data harmonisation and resolve inconsistent taxonomy are essential, while, for new data standardised and reusable archiving practices should be encouraged. The latter can be achieved through the adoption of community-defined (meta)data standards by researchers and data stewards. The implementation and use of such standards helps to facilitate data interoperability, reusability, and syntheses (Wieczorek et al., 2012).

Existing standards, such as DarwinCore (Wieczorek et al., 2012) and PaCTS (Paleoclimate Community reporTing Standard; Khider et al., 2019), have been influential in the standardisation of biodiversity and paleoclimate (meta)data. PaCTS already lists some properties regarding micropalaeontological assemblage data that are deemed essential for data standardisation and there has been extensive efforts on resolving the inconsistent taxonomy of planktonic foraminifera including recommendations to increase the reusability and interoperability of sedimentary microfossil data (Brummer and Kučera, 2022). Though, there is still a lack of consistent community-defined (meta)data standards for assemblage data of all marine groups that produce microfossils, as the existing community-defined (meta)data standards are not sufficient to fully encompass the complexities of microfossil assemblage data. While DarwinCore and PaCTS have made significant contributions to biodiversity and paleoclimate data standardisation, they are not comprehensively addressing the unique challenges posed by microfossil assemblage data. For instance, PaCTS focusses on inferred paleoclimate data rather than assemblage data, while DarwinCore is specifically designed for the standardisation of species occurrences and does not directly capture information about relative abundances of species or the composition of species assemblage. This study highlights the importance of developing comprehensive (meta)data standards for micropalaeontological assemblage data, ultimately fostering data interoperability, reusability, and synthesis in the field.

However, developing comprehensive (meta)data standards for micropalaeontological assemblage data necessitates the understanding of the prevailing challenges and issues during data harmonisation. This study aims to address the current state of planktonic foraminifera data harmonisation by identifying and mapping common problems and challenges by focusing on the Quaternary, thus only extant species with no new species or extinctions. This study is the result of the manual curation and harmonisation of the planktonic foraminifera time series used in this thesis (see Chapters 1.5.1 and 3.4.1) and the extensive screening of planktonic foraminifera assemblage datasets that has been conducted as part of the NFDI4Earth pilot "Reusability of data with complex semantic structure" (Strack et al., 2023). For this project we worked together with PANGAEA, an open-access information system with a 30-year history and has the goal to support research data management and provide long-term data archiving and publication. All data and metadata are curated by domain expert data editors and structurally harmonised and checked for completeness and plausibility in close collaboration with the submitting scientists (Felden et al., 2023). For this pilot, roughly 2,400 planktonic foraminifera data files that are publicly available at PANGAEA have been analysed.

This manuscript serves as a detailed showcase of the common challenges and problems associated with legacy sedimentary planktonic foraminifera count data, highlighting the need for community-defined (meta)data standards for marine microfossil assemblage data. Additionally, we propose an automated solution for harmonising count data of extant planktonic foraminifera publicly available on PANGAEA, along with examples of an ideal (legacy) dataset.

## 6.2 Common problems and challenges with legacy datasets

The common problems and challenges associated with the standardisation of planktonic foraminifera assemblage datasets can be divided into two main groups: taxonomic issues and archiving issues. The most common taxonomic issues can be attributed to the use of synonyms. An initial scan of the 2,400 planktonic foraminifera assemblage data files yielded 230 different names for extant planktonic foraminifera species. This is quite astonishing considering that only around 50 extant planktonic foraminifera morphospecies are generally recognized (Brummer and Kučera, 2022) and emphasises the need for taxonomic harmonisation when datasets are combined. Semantically complex micropalaeontological data also often leads to specific archiving challenges, such as the use of duplicated names due to unclear taxonomy or taxa grouping, archiving of grouped taxa, and the intricate preservation of important taxonomic information. Further archiving issues are introduced by reporting relative rather than absolute abundances. Some of these issues may result from the archiving process itself and which have gone unnoticed during cross-checking by uploaders before publication. In the following paragraphs, these specific problems and challenges are explained in more detail and, where appropriate, illustrated with data examples. All data examples are from datasets that are publicly available on PANGAEA and have been anonymised to highlight the actual issues encountered, rather than focusing on specific datasets or authors. If not stated otherwise, we follow the nomenclature of Brummer and Kučera (2022), because it is the latest that also considers genetic data.

### 6.2.1 Taxonomic issues

The most common taxonomic issues in planktonic foraminifera stem from the use of synonyms, as a result of different taxonomic schools and ever-evolving taxonomic insights, leading to the continuous revision of taxonomic concepts. The mapping of these synonyms can be divided into three categories: one-to-one, many-to-one and one-to-many (Figure 6-1).

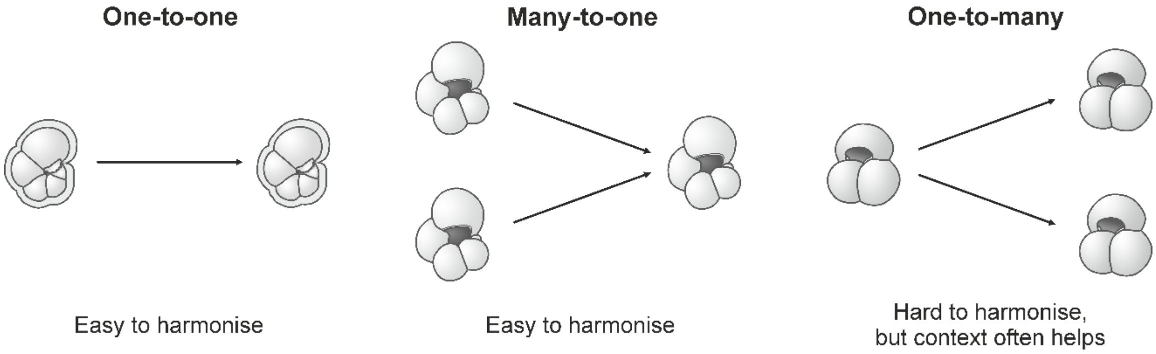


**Figure 6-1:** Many taxonomic issues during data harmonisation are caused by the use of synonyms which can be divided into three categories. One-to-one synonyms are names with an unambiguous direct relationship, many-to-one synonyms occur when several names are used for the same taxa and one-to-many synonyms are names that may refer to multiple distinct taxa. While one-to-one and many-to-one synonyms are relatively easy to harmonise, one-to-many synonyms are hard to harmonise but context often helps.

One-to-one synonyms are species names with an unambiguous direct relationship and are therefore easy to harmonise. For instance, *Globigerinella siphonifera* and *Globigerinella aequilateralis* are one-to-one synonyms that describe the same taxon (Brummer and Kučera, 2022). Also, relatively easy to harmonise are many-to-one synonyms that occur when several names are used for the same taxon. For instance, *Orbulina universa*, *Orbulina suturalis* and *Biorbulina bilobata* may have been described in a modern sediment sample, but all three names refer to the same extant taxon with *O. suturalis* and *B. bilobata* being rare morphological variants of *O. universa*, that have inaccurately been upgraded to species status (Brummer and Kučera, 2022). This is also a useful example to emphasise that taxonomic harmonisation of planktonic foraminifera becomes even more difficult and cumbersome when also including extinct species, because there is an extinct planktonic foraminifera species, rather than variant, named *O. suturalis* that occurred around 15 million years ago (Wade et al., 2011). Hard to harmonise as they lead to profound ambiguity are one-to-many synonyms where one name may refer to multiple distinct taxa. Sometimes a lack of taxonomic consensus is the reason for one-to-many synonyms, but more often these types of synonyms are caused by real and new taxonomic insights leading to changing taxonomic concepts and adopting these new concepts needs time. An example for a one-to-many synonym is *Globigerinoides ruber* as this name might refer to the taxon *Globigerinoides ruber* or to the taxon *Globigerinoides elongatus* (see paragraph "*Globigerinoides ruber* - elongatus complex" below for a more detailed description). Context may often help with the harmonisation of these different variations of taxonomic synonyms, especially with one-to-many synonyms. Most of these issues are caused by only a handful of species (complexes). These are the *Globigerinoides ruber - elongatus* complex, the Neogloboquadrinid complex and the species *Trilobatus sacculifer*. Because these complexes cause most of the taxonomic confusion, solving these complexes makes all the difference in successfully reusing extant planktonic foraminifera microfossil data.

#### *6.2.1.1 Globigerinoides ruber - elongatus complex*

The most notorious trouble maker, when it comes to the taxonomic harmonisation of planktonic foraminifera, is the *Globigerinoides ruber* - *elongatus* complex (Plate 6-1). It is a suitable example that clearly shows the complexity of the harmonisation of planktonic foraminifera legacy data, because it often produces one-to-many synonym issues that are mainly caused by changing taxonomic concepts and quite recent new taxonomic insights. In the first half of the 19th century, the French naturalist d'Orbigny firstly described *Globigerinoides elongatus* (d'Orbigny, 1826) and *Globigerinoides ruber* (d'Orbigny, 1826). Even though d'Orbigny specifically highlighted the reddish pigmentation of *G. ruber* tests, the name was soon used to also describe specimens that lacked the red pigmentation (see Aurahs et al., 2011). A taxonomic revision by Parker (1962) lumped extant specimens of *G. elongatus* because of their morphological similarities with *G. ruber*, which led to the subsequent disappearance of the name *G. elongatus* in modern planktonic foraminifera research until it was reinstated after a combined morphological and genetic investigation by Aurahs et al. (2011). Recently, Morard et al. (2019) genetically distinguished the extant lineage of G. ruber without the red pigmentation from the extant lineage of *G. ruber* with the red pigmentation thus leading to the establishment of two *G. ruber* subspecies which were previously called variants: *Globigerinoides ruber albus* Morard et al., 2019 and *Globigerinoides ruber ruber* (d'Orbigny, 1826). Finally, some datasets distinguish a morphologically variant with a high-spired form (often referred to as *G. ruber pyramidalis* or *G. ruber* high-spired) that can occur in *G. ruber albus*, *G. ruber ruber* and *G. elongatus* (Brummer and Kučera, 2022). As it occurs in all three taxa, it can never be resolved correctly; fortunately, we only recorded it in 23 out of the roughly 2,400 datasets and when reported this variety has only been counted in very low abundances.

Consequently, the broadening and successive narrowing of the taxonomic concept of the *Globigerinoides ruber - elongatus* complex through time clearly illustrates the complexity that may occur during taxonomic data harmonisation and emphasise the importance of metadata information on the taxonomic concepts that have been followed during the initial data acquisition.

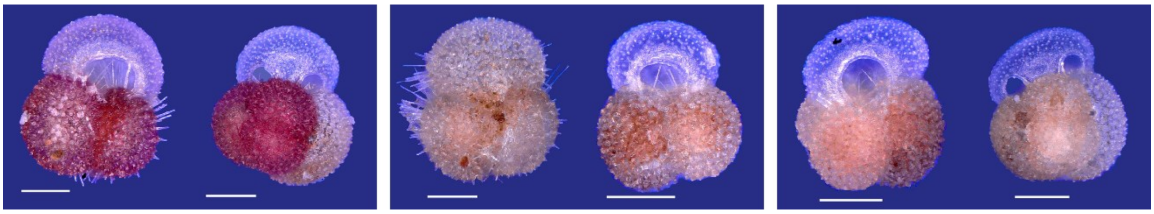


**Plate 6-1:** Left: *Globigerinoides ruber ruber* (d'Orbigny, 1836), middle: *Globigerinoides ruber albus* Morard et al., 2019, right: *Globigerinoides elongatus* (d'Orbigny, 1826). Scale bar: 100 µm. Images taken with permission from Lessa et al. (2020).

Since *G. elongatus* was only reinstated as a distinct extant taxon quite recently (Aurahs et al., 2011) and due to its morphologically similarities with *G. ruber albus*, there is a large amount of datasets where these two taxa are not distinguished. Hence, if not otherwise stated, it needs to be assumed that the counts of *G. ruber* are actually the sum of *G. ruber* and *G. elongatus*. Furthermore, since the subspecies concept of *G. ruber* is very new (Morard et al., 2019) and the formerly white and red/pink variants have not always been accounted for, there are also many datasets where *G. ruber albus* and *G. ruber ruber* are not differentiated.

To harmonise these datasets to the highest possible taxonomic level and resolve these one-to-many issues, detailed information on the (meta)data is essential. For instance, to resolve the taxon name *G. ruber* in a specific dataset, we need to know whether *G. elongatus* is present or absent. Also, information of the geographic location and age of the sample(s) are important, because *G. ruber ruber* went extinct in the Pacific and Indian Ocean around 120 ka ago (Thompson et al., 1979).

As an example, imagine two example datasets that both report *G. ruber*. The first dataset covers the past 10,000 years, is located in the Pacific Ocean and additionally reports *G. elongatus*, while the second dataset is located in the Atlantic Ocean but does not report *G. elongatus*. So, even though both datasets report *G. ruber*, in the first example the name *G. ruber* refers to the subspecies *G. ruber albus*, because *G. elongatus* is reported next to *G. ruber* and *G. ruber ruber* does not occur in the Pacific Ocean during the past 10,000 years, and taxonomy can be resolved to subspecies level. In the second example such taxonomic precision to subspecies level cannot be attained and the taxonomy in fact remains ambiguous as it cannot be excluded that counts of *G. ruber* also include *G. elongatus*. These are only two of the several one-to-many issues that we observed in this complex. Figure 6-2 shows a cross-functional flowchart that addresses and resolves all of the observed taxonomic issues in this complex to the highest possible level and retains ambiguity whenever species cannot be reliably separated.

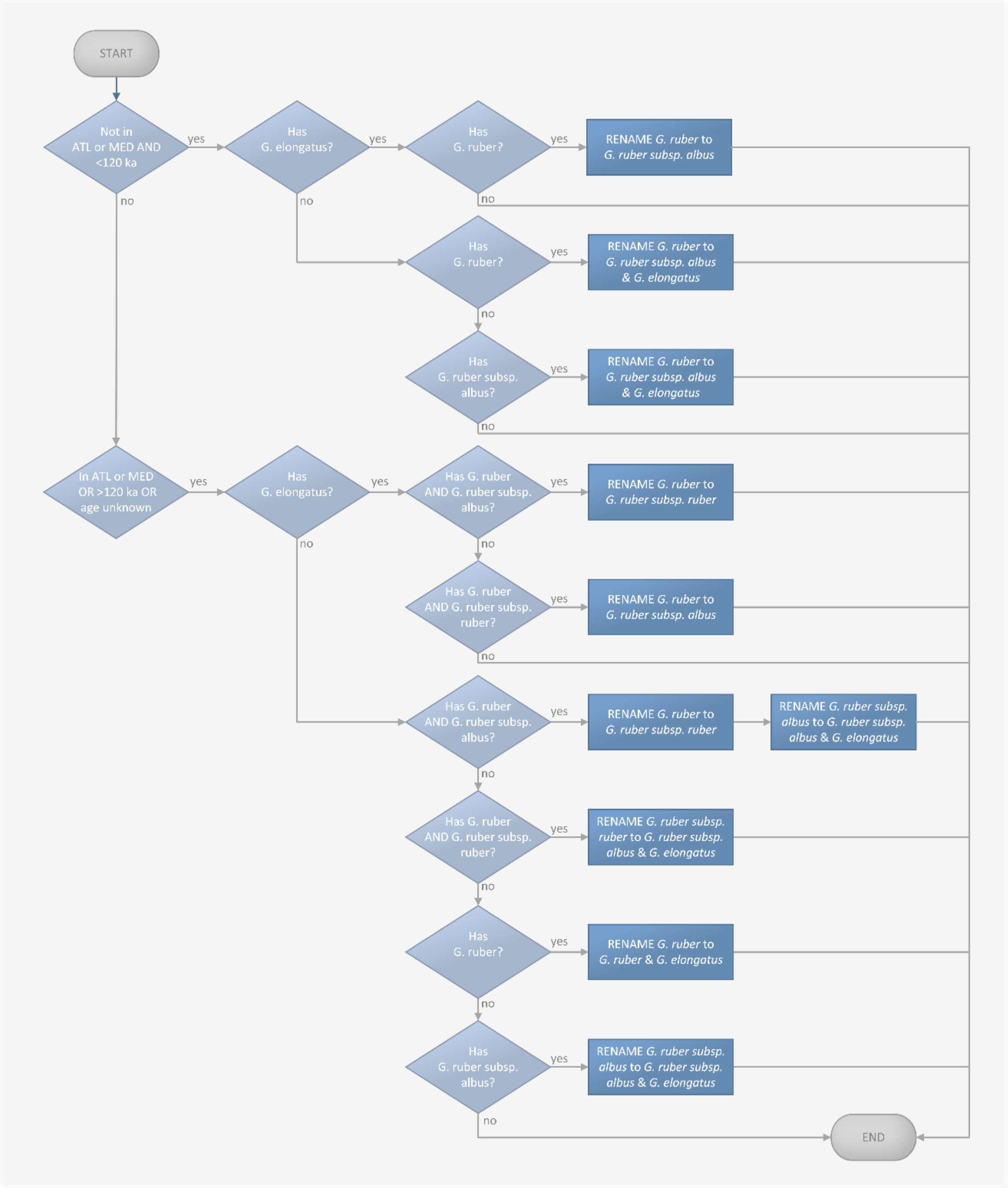


**Figure 6-2:** Cross-functional flowchart of the Globigerinoides ruber - elongatus complex that addresses and resolves all taxonomic issues observed in this complex. ATL: Atlantic Ocean, MED: Mediterranean Sea.

### *6.2.1.2 Neogloboquadrinid complex*

The Neogloboquadrinid complex (Plate 6-2) is another species complex that causes a lot of ambiguity and taxonomic issues during data harmonisation. This complex includes the species *Neogloboquadrina dutertrei* (d’Orbigny, 1839), *Neogloboquadrina pachyderma* (Ehrenberg, 1862) and *Neogloboquadrina incompta* (Cifelli, 1961). Right after its initial description, the predominantly right-coiling (dextral) *N. incompta* was synonymised with the predominantly left-coiling (sinistral) *N. pachyderma* by Parker (1962) as it was considered a phenotypic variant rather than a distinct taxon. The two variants were subsequently mostly distinguished by the indication of their coiling direction (i.e., *N. pachyderma* dextral and *N. pachyderma* sinistral), though some researchers still used the original name coined by Cifelli. *N. incompta* was reinstated as a distinct species due to genetic differences between the two variants by Darling et al. (2006). Furthermore, Kipp (1976) introduced the long-used P/D (pachyderma/dutertrei) intergrade as an intermediate form between *N. dutertrei* and *N. pachyderma* dextral. However, this form has no taxonomical validation, being defined for operational purposes, and it is nowadays assumed that most specimens of this category are considered to be *N. incompta* (Kucera et al., 2005b).

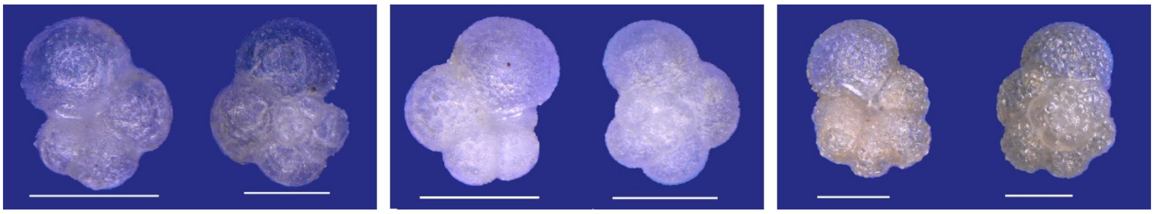


**Plate 6-2: Left:** *Neogloboquadrina incompta* (Cifelli, 1961), middle: *Neogloboquadrina pachyderma* (Ehrenberg, 1862), right: *Neogloboquadrina dutertrei* (d'Orbigny, 1839). Scale bar: 100 µm. Images taken with permission from Lessa et al. (2020).

Unfortunately, this complex leaves some instances where a simple resolution is not possible. This occurs for example when only *N. pachyderma* but not *N. incompta* is reported in the data and no indication of the coiling direction is given. Here, the user is forced to make a decision based on the original publication and the available metadata such as the age of the dataset itself and information on the taxonomic concept that has been followed. The geographic location of the site can further help to make a more sophisticated decision, because *N. pachyderma* mainly occurs in polar to subpolar waters whereas *N. incompta* occurs in temperate to subpolar waters. In the described example above, the decision could be to either retain *N. pachyderma* (e.g., the site is located in the Arctic Ocean), or to rename it to *N. incompta* (e.g., the site is located in the mid-Atlantic Ocean). In some cases, there may not be enough information available to resolve the ambiguity. In such cases, one could for simplicity consider all occurrences of the taxon *N. pachyderma* as the species *N. pachyderma* (as is done in the Triton database), but, for consistency (with datasets that have distinguished the two species) we favour preserving the ambiguity in the name and only lump when the analysis requires this (Figure 6-3).

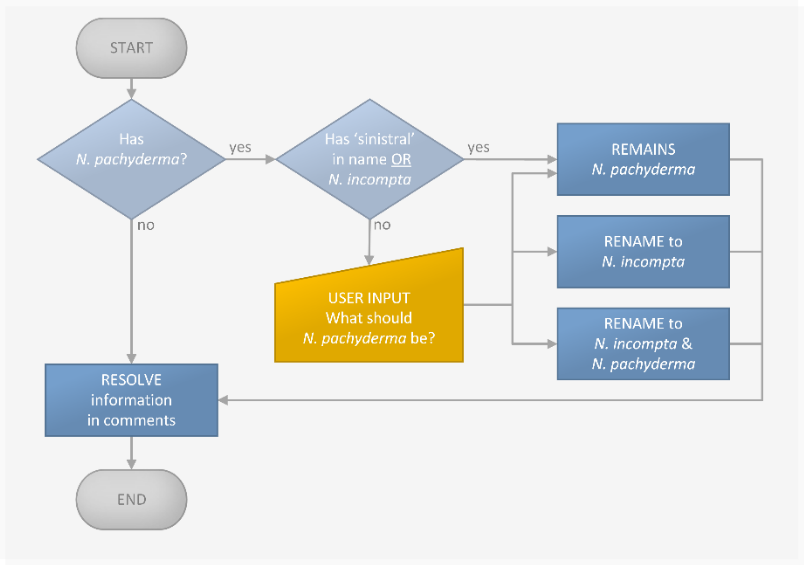


**Figure 6-3:** Cross-functional flowchart of the Neogloboquadrinid complex highlighting instances where a simple resolution is not possible and user input is needed.

### 6.2.1.3 *Trilobatus sacculifer*

*Trilobatus sacculifer* (Brady, 1877) is another species that causes some ambiguity while working with extant planktonic foraminifera species. Despite being genetically very homogeneous (André et al., 2016), *T. sacculifer* is a species that shows a wide range of morphological variability mostly concerning the form of the final chamber (Plate 6-3), which has led to the usage of many different names and synonyms for morphological variants (Table 6-1). Additionally, the genus *Trilobatus* was just established quite recently due to fossil and genetic evidence (Spezzaferri et al., 2015), leading to even more naming inconsistencies. When working with extant planktonic foraminifera, all these different synonyms can be easily resolved to *T. sacculifer*, because there is no evidence that there is more than one extant *Trilobatus* species (Brummer and Kučera, 2022). However, data harmonisation would become way more cumbersome when the information on the morphological variants should be preserved, especially because of the naming inconsistencies (see Table 6-1).

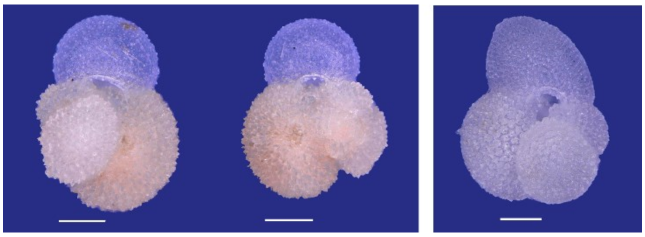
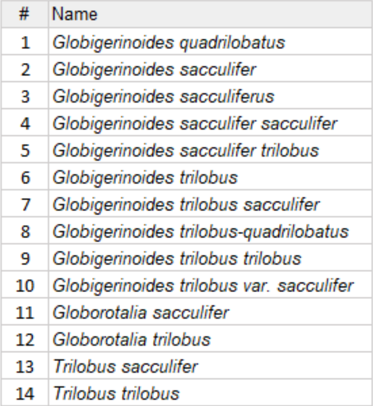


**Plate 6-3:** Left: *Trilobatus sacculifer* (Brady, 1877) without sac-like last chamber, right: *Trilobatus sacculifer* (Brady, 1877) with sac-like last chamber. Scale bar: 100 µm. Images taken with permission from Lessa et al. (2020).

**Table 6-1:** Synonyms of *Trilobatus sacculifer* observed during the data harmonisation of the planktonic foraminifera time series used in this study.



| # | Name |
|---|---|
| 1 | *Globigerinoides quadrilobatus* |
| 2 | *Globigerinoides sacculifer* |
| 3 | *Globigerinoides sacculiferus* |
| 4 | *Globigerinoides sacculifer sacculifer* |
| 5 | *Globigerinoides sacculifer trilobus* |
| 6 | *Globigerinoides trilobus* |
| 7 | *Globigerinoides trilobus sacculifer* |
| 8 | *Globigerinoides trilobus-quadrilobatus* |
| 9 | *Globigerinoides trilobus trilobus* |
| 10 | *Globigerinoides trilobus var. sacculifer* |
| 11 | *Globorotalia sacculifer* |
| 12 | *Globorotalia trilobus* |
| 13 | *Trilobus sacculifer* |
| 14 | *Trilobus trilobus* |

### 6.2.2 Archiving issues

Apart from the taxonomic issues that are often not easy to resolve, the analysis of the 2,400 data files also revealed that semantic complexity in micropalaeonto-logical data often leads to archiving errors, further complicating data reusability. Many of these archiving errors can be attributed to duplicated names, the archiving of grouped taxa, the archiving of additional taxonomic information and the usage of relative abundances.

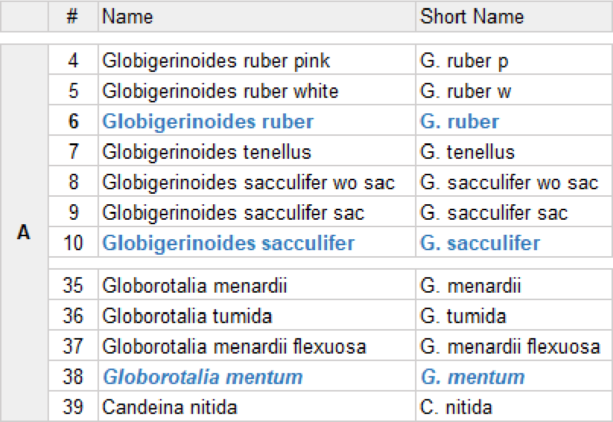
#### *6.2.2.1 Archiving of grouped taxa*

When it comes to data archiving and increasing the reusability of data in general, it is always good to give as much information as possible. However, it is as equally important to not give redundant information as this further increase data complexity and may introduce preventable archiving issues. Some of these preventable issues are introduced due to the archiving of grouped taxa, which might be the result of previous attempts to harmonise data but where kept when archiving the data itself. Data example A (Table 6-2) shows several instances where subspecies or variants of taxa are reported. For instance, data example A reports *G. ruber* pink (synonym for *G. ruber ruber*), *G. ruber* white (synonym for *G. ruber albus*) but also their sum as *G. ruber*. The same holds for *G.*

*sacculifer* (synonym of *T. sacculifer*) which is the sum of the reported morphological variants with and without a sac-like final chamber. These summed columns need to be identified and resolved during data harmonisation and before data analysis, because the risk is high that otherwise both the summed columns and the individual columns are unintentionally kept in the dataset which would lead to doubled species abundances and a changed assemblage. The resolution of these grouped taxa columns is possible, but requires extra processing steps such as sum checks. However, these sums often do not add up due to rounding issues or real archiving errors, causing extra confusion.

Data example A (Table 6-2) also reports an interesting scientific oddity that was caused by the (redundant) grouping of taxa and the use of abbreviations: *Globorotalia mentum*. For people who have no previous experience with extant planktonic foraminifera species, this would probably go unnoticed. The problem is: *G. mentum* is not a valid taxon. It is the summed group of *G. menardii* (synonym of *G. cultrata*) and *G. tumida* and was abbreviated to *G. mentum* ("men" from *G. menardii* and "tum" from *G. tumida*). This problem could have been prevented if only the constituent taxa would have been reported or by a clearer description of how taxa were lumped. Although the identification of these issues is straightforward through cross-referencing with valid species, determining their actual nature becomes challenging. It requires that the constituent species are adequately reported in the dataset and that sums of two or more species can be unambiguously assigned to a single category.

**Table 6-2:** Data example A reporting grouped taxa (**bold**) and a meaningless species name that is caused by unclear taxonomy (***bold and italic***).

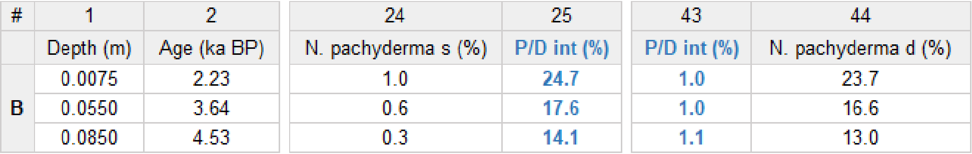


| | # | Name | Short Name |
|---|---|---|---|
| A | 4 | Globigerinoides ruber pink | G. ruber p |
| | 5 | Globigerinoides ruber white | G. ruber w |
| | **6** | **Globigerinoides ruber** | **G. ruber** |
| | 7 | Globigerinoides tenellus | G. tenellus |
| | 8 | Globigerinoides sacculifer wo sac | G. sacculifer wo sac |
| | 9 | Globigerinoides sacculifer sac | G. sacculifer sac |
| | 10 | **Globigerinoides sacculifer** | **G. sacculifer** |
| | 35 | Globorotalia menardii | G. menardii |
| | 36 | Globorotalia tumida | G. tumida |
| | 37 | Globorotalia menardii flexuosa | G. menardii flexuosa |
| | 38 | ***Globorotalia mentum*** | ***G. mentum*** |
| | 39 | Candeina nitida | C. nitida |

### Additional complication due to duplicate names

The occurrence of duplicate (non-unique) names in planktonic foraminifera datasets can be attributed to unclear taxonomy, the grouping of taxa, and missing additional taxonomic information. Often the same species name is being used for different (groups of) taxa, which results in the same column names despite containing different data. We found non-unique taxon names in 400 (i.e., 17 %) out of the 2,400 investigated data files. Data example B (Table 6-3) reports two columns as P/D intergrade, but both columns contain different data, indicating that one of these columns does not refer to only specimens of P/D intergrade. To resolve these duplicated names and identify possibly redundant columns, the data itself needs to be checked. In particular, it needs to be checked whether one column is the sum of some other columns, to figure out which column might contain redundant data. After inspecting the data in data example B, it becomes clear that the first P/D intergrade column (#25) is the sum of the second P/D intergrade column (#43) plus the *N. pachyderma* dextral (synonym of *N. incompta*) column (#44) meaning that the first P/D intergrade column (#25) is redundant, because all information is already given in the other two columns. Consequently, context and the data itself can help to resolve most of these duplicated name issues, but it often requires additional work and processing steps. While such examples may appear trivial and easily identifiable, they pose challenges to the machine readability of the data.

**Table 6-3**: Data example B reporting columns with duplicated names (**bold**) despite containing different data.

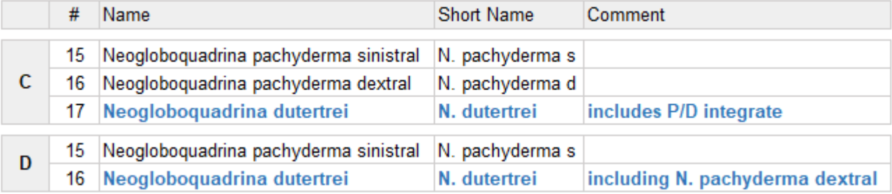


| # | 1 | 2 | 24 | 25 | 43 | 44 |
|---|---|---|---|---|---|---|
| | Depth (m) | Age (ka BP) | N. pachyderma s (%) | **P/D int (%)** | **P/D int (%)** | N. pachyderma d (%) |
| **B** | 0.0075 | 2.23 | 1.0 | **24.7** | **1.0** | 23.7 |
| | 0.0550 | 3.64 | 0.6 | **17.6** | **1.0** | 16.6 |
| | 0.0850 | 4.53 | 0.3 | **14.1** | **1.1** | 13.0 |

### Archiving of additional taxonomic information

In some cases, datasets may contain valuable taxonomic information in the comment section of the parameter file (Table 6-4). This information is appreciated, because it means that the taxonomy can be harmonised to a higher taxonomic level. However, we recommend that this information about the grouping of taxa be reflected in the column names rather than providing names that refer to only one of the constituent taxa. This is crucial because such grouped taxa names might overshadow the additional taxonomic information, as only the short names are presented as data column headers. Consequently, there is a risk that this value taxonomic information might be overlooked when working with the data, even though it is necessary to correctly resolve specific taxa during data harmonisation to the highest possible taxonomic level. For instance, data example C states that P/D intergrade (which is nowadays considered to be *N. incompta*) is included in *N. dutertrei* and data example D states that *N. pachyderma* dextral (synonym for *N. incompta*) is included in *N. dutertrei* (Table 6-4). So, even though both data column headers state *N. dutertrei*, they actually refer to *N. dutertrei* and *N. incompta*.

**Table 6-4:** Data examples C and D that contain valuable taxonomic information in the comment section (**bold**).



| | # | Name | Short Name | Comment |
|---|---|---|---|---|
| C | 15 | Neogloboquadrina pachyderma sinistral | N. pachyderma s | |
| | 16 | Neogloboquadrina pachyderma dextral | N. pachyderma d | |
| | 17 | **Neogloboquadrina dutertrei** | **N. dutertrei** | **includes P/D integrate** |
| D | 15 | Neogloboquadrina pachyderma sinistral | N. pachyderma s | |
| | 16 | **Neogloboquadrina dutertrei** | **N. dutertrei** | **including N. pachyderma dextral** |

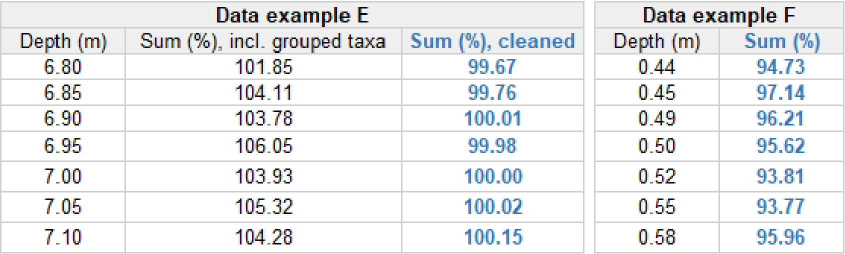
### *6.2.2.2 Relative abundances*

The majority of the 2,400 investigated datasets and 76 % of the datasets used in this thesis report their planktonic foraminifera counts in relative abundances rather than raw counts (integers). One reason for this might be that absolute abundances are difficult to compare because of very different and often poorly constrained accumulations rates. This means that normalisation is needed for most analysis, but does not warrant the archiving of relative abundances. An additional but less reputable reason might be that relative abundances make it easier to mask poor microfossil concentrations or preservation, because relative abundance data omits important information about the reliability and quality of the data itself (e.g. minimum count), which might severely undermine the credibility of study results and hinder data reproducibility as proven by (Telford, 2019a; Telford, 2019b).

Unfortunately, the archiving of (only) relative abundances can cause a lot of issues especially when reusing the data. Percentages are reported in decimal places (mostly two, but sometimes only one), therefore introducing rounding errors that accumulate over time when the data is reused. More serious errors are often caused by the double counting of (grouped) taxa, which cannot always be corrected (Table 6-5). Data example E contains grouped species columns and calculating the sum yields values beyond 100 %. Even after accounting for the grouped species columns the sum deviates from 100 %. These smaller discrepancies could be attributed to rounding errors. Data example F reports no grouped columns, but the sum deviates significantly from 100 %. Here, the issue might be a missing column, most likely a column that contains unidentified specimens. Even though it is impossible to know for sure what is in the missing column, it is an indication that the reported counts are incomplete. If the missing column in data example F is the unidentified specimen column, the ratio of the species abundances is unaffected, meaning the issue can be resolved by extra processing steps if the data is reused and the information on the missing column is not needed in further data analysis.

Collectively, the tendency to report relative abundances rather than absolute raw counts, coupled with the practice to include counts of both individual and grouped species in the same dataset, has led to an enormously high amounts of archived datasets that contain errors. Of the approximately 43,000 assemblages with relative abundances we analysed, only half of the sums of percentages added up to 100 ± 5 %. It should be noted that the issue of missing columns can also arise with raw counts, but without the inclusion of count sums, such discrepancies might go unnoticed. This emphasises the need to advance the field by developing comprehensive (meta)data standards that are universally adopted by the entire community. Standardisation efforts will enhance data quality, reliability, and reusability of micropalaeontological assemblage data in future research.

**Table 6-5:** Calculated sums (**bold**) of data examples E and F that illustrate the disadvantages of reporting relative abundances.



| Data example E | | | Data example F | |
|---|---|---|---|---|
| Depth (m) | Sum (%), incl. grouped taxa | **Sum (%), cleaned** | Depth (m) | **Sum (%)** |
| 6.80 | 101.85 | **99.67** | 0.44 | **94.73** |
| 6.85 | 104.11 | **99.76** | 0.45 | **97.14** |
| 6.90 | 103.78 | **100.01** | 0.49 | **96.21** |
| 6.95 | 106.05 | **99.98** | 0.50 | **95.62** |
| 7.00 | 103.93 | **100.00** | 0.52 | **93.81** |
| 7.05 | 105.32 | **100.02** | 0.55 | **93.77** |
| 7.10 | 104.28 | **100.15** | 0.58 | **95.96** |

## 6.3 R pipeline to harmonise planktonic foraminifera taxonomy of legacy data

A wealth of microfossil assemblage data is available through open data sharing, with many of these datasets archived in dedicated public repositories such as PANGAEA or NOAA’s World Data Service for Paleoclimatology. These repositories are of immense importance for data preservation, quality, and consistency, through curation and quality control protocols, as well as standardisation of data formats and metadata. As a result, data accessibility and interoperability are enhanced. While these repositories serve as valuable tools for identifying and accessing suitable datasets, the harmonisation of microfossil assemblage legacy data remains challenging and requires extensive manual work. Taxonomic issues need to be resolved, the data need to be checked for duplicated names and grouped taxa and sometimes metadata need to be analysed. Within the scope of the NFDI4Earth pilot "Reusability of data with complex semantic structure" we developed an R pipeline (https://zenodo.org/record/8124240) to provide the community with a solution to automatically download and harmonise legacy taxonomic data of extant planktonic foraminifera that are publicly available on PANGAEA. Our script goes beyond the simple synonymisation of taxa names, because it also downloads the desired dataset and linked metadata directly from PANGAEA using the corresponding persistent identifier (DOI), checks the data and resolves most of the issues that have been described throughout this manuscript and harmonises the data while retaining the original taxonomy.

The current version of the script relies on an external dictionary and the classification scheme of the harmonised taxonomy follows the ontology of WoRMS (World Register of Marine Species). WoRMS is a comprehensive register of valid taxa names of marine organisms including information on synonyms that is quality controlled by taxonomic experts. It also contains information on the higher classification in which each scientific name is linked to its parent taxon (WoRMS Editorial Board, 2023). Each available name in WoRMS has a unique and stable identifier (AphiaID) that can be easily accessed via machine-to-machine services which makes it a powerful tool for taxonomic data harmonisation (Vandepitte et al., 2015). Since PANGAEA already links a considerable amount of its parameter (species) names to AphiaIDs using an automatized parameter annotation service (see also Diepenbroek et al., 2017), we use these AphiaIDs to match the taxa list in the legacy datasets with the standard register of WoRMS and retrieve the accepted taxon names and resolve the identity of unaccepted synonyms. The current automatized parameter annotation service of PANGAEA, however, shows a certain margin of error and, in particular, makes incorrect assignments for the abovementioned complexes. We therefore used our specialist knowledge and manually reassigned some previously incorrectly assigned annotations within the PANGAEA's metadata and curated a list of synonyms for taxa in PANGAEA that are not yet linked to WoRMS to resolve taxonomic confusion. We improved PANGAEA's parameter annotation service (https://ws.pangaea.de/param-annotator/) for which we identified e.g. difficulties to recognise species names which may include optional subgenus names and work towards an integration of RDA I-ADOPT concepts within this service (see Magagna et al., 2022). With these further improvements in the internal PANGAEA annotation service, the use of the manually curated synonym list should become obsolete in the future.

Currently, the script only works for extant planktonic foraminifera meaning that the species pool remained stable. Extending the script to also be applicable to data from deep time would lead to more even ambiguity during data harmonisation, because synonyms vary with time as we showed in the example of *O. suturalis* (see "Archiving issues"). Including data from deep time would mean that age information for the datasets would be needed to resolve the taxonomic issues, but which is often not available in the same data file as the assemblage data making it essential to better link datasets from the same time series. The application of the script to deep time would also require information on the stratigraphic range of taxa, which is currently not available through PANGAEA, and which would therefore need to be gathered from external sources such as mikrotax (www.mikrotax.org).

In principle, the R script can also be adapted to work with other data that is not from PANGAEA. For this, it would need to be changed in a way that it downloads the data and corresponding metadata from other repositories or imports the (meta)data from an already existing file. Furthermore, it needs to be tested whether all occurring taxon names are part of the external dictionary, though the script already helps with that, because in a first step it should drop all columns that contain no species abundance data. If it drops a column that contains abundance data, this name needs to be added to the external dictionary.

## 6.4 The ideal planktonic foraminifera assemblage dataset

The progress of paleoclimate and micropalaeontological research is tied to the standardisation of scientific data and, in recent years, much work has been done to increase the FAIRness of scientific data and many recommendations and best practices on data handling and archiving have been developed (e.g., Wieczorek et al., 2012; Wilkinson et al., 2016; Khider et al., 2019; Jonkers et al., 2020). For planktonic foraminifera in particular, Brummer and Kučera (2022) have given very useful information on the operational taxonomy of planktonic foraminifera. We fully approve their taxonomic recommendations with the exception of the reporting of redundant grouped taxa columns. Based on our new experience, we strongly discourage from reporting grouped taxa when the constituent taxa are reported individually, as it increases data complexity and necessitates additional processing steps when reusing the data. If the sum of specific taxa or variants is needed in subsequent data analysis, then this can be easily calculated as a derivative from the archived data.

The following list contains information of a planktonic foraminifera assemblage dataset that we consider ideal for reuse. Additional information that is only applicable for new datasets is indicated by a leading asterisk and italic font.

- All work(s) on which the taxonomy is based on is(are) cited and any deviations are clearly indicated. A full list of species that have been considered is given even if absent.
- Full taxon names (i.e., no abbreviations) are given
- Each reported taxon name is matched with an AphiaID (new and legacy data) and original taxonomy is preserved (legacy data)
- Full assemblage is counted to the highest possible taxonomic level
- All taxa and unidentified species are reported including taxa that are absent
- No redundant grouped columns are reported (i.e., the constituent taxa are reported individually)
- Necessary columns that report grouped taxa (i.e., the constituent taxa are <u>not</u> reported individually) are named in a way that allows for unambiguous identification of the constituent taxa
- Absolute raw counts are given
- All metadata associated with the assemblage counts are given (i.e., sampling depth, split, size fraction, preservation, possible sediment treatments, counting method)
- All metadata associated with the sediment core are given (i.e., unambiguous site name, site location, water depth, sampling campaign, sampling method, collection date, details about chronology, description of environmental and depositional setting)
- **All associated metadata described above is made available alongside the digitally available data*
- **Irrespective of the initial study purpose, the data is preserved in a way that ensures maximal data reusability and long-term archival*

## 6.5 Concluding remarks

In this manuscript we showcased the common problems and challenges that may arise when reusing publicly available planktonic foraminifera assemblage datasets and give an example of an ideal dataset. We also provided the community with an R script to automatically harmonise extant planktonic foraminifera assemblage data that is available at PANGAEA to contribute to the improvement of the reusability and interoperability of planktonic foraminifera assemblage data. We further emphasise that different solutions are needed for legacy data that is already in the public domain and new data submissions and highlight the need for community-derived (meta)data standards for microfossil assemblage data.

Even though this manuscript focuses on very specific data (i.e. planktonic foraminifera assemblage data), heterogeneous data with complex semantic structures or lack of standardised vocabularies are a common problem in many paleoclimate and biodiversity research communities (Khider et al., 2019; Jonkers et al., 2020). Community-defined (meta)data standards need to be developed that are then applied by both researchers and data stewards. We therefore initiated a community-consultation process (in the form of a survey) to formulate micropalaeontological (meta)data standards. It is our intention to make these guidelines useful for the entire micropalaeontological research community.

This manuscript deals with the improvement of the reusability and interoperability of micropalaeontological data, still there is a lot of dark micropalaeontological data that remains unfindable and inaccessible. This applies especially to older datasets generated before the era of digitalisation and good data stewardship practices. To rescue this old and invisible data, more targeted community-wide efforts are needed before the generation of scientists who generated these data retires. A notable portion of micropalaeontological data used today also remains inaccessible as only derived products are made available (e.g., Jonkers et al., 2020). Our challenge thus remains to increase the FAIRness of micropalaeontological data to fully unlock their potential in putting the current biodiversity crisis in a long-term context.

## 6.6 Data availability

The R script to harmonise extant planktonic foraminifera datasets that are publicly available at PANGAEA is available on GitHUB (https://github.com/lukasjonkers/harmonisePFTaxonomy/tree/v1) and Zenodo (https://zenodo.org/record/8124240). Further information on the NFDI4Earth pilot "Reusability of data with complex semantic structure" as well as a cross-functional flowchart and in-depth description of the R script are available on Zenodo (https://zenodo.org/record/8124211).

# 7

# Extended discussion

The overarching goal of this thesis was to assess the long-term response of marine plankton to past climate change that is comparable in magnitude to predicted future climate change. To achieve this, the sedimentary record of planktonic foraminifera from the North Atlantic Ocean was utilised and assemblage composition changes from the last cold stage to the current warm period were investigated. Moreover, specific hypotheses related to the long-term response of marine plankton to climate change, with a particular emphasis on SST as a measure of climate variability, were tested. The initial hypotheses guided this research and provided valuable insights into past biodiversity changes in response to climate change, while also leaving several open questions that have emerged from the results. This extended discussion begins with a summary of the main results by referring back to the initial hypotheses presented in Chapter 1.4, followed by a comprehensive discussion of some of the open questions that have emerged.

## 7.1 Summary of main hypotheses findings

### H1: Planktonic foraminifera assemblage change is in equilibrium with SST change

The comparison of overall planktonic foraminifera assemblage change in the North Atlantic Ocean from the last cold stage to the current warm period with global mean SST revealed that these assemblages began to change with the onset of global warming around 17 ka ago. However, contrary to our initial expectations, planktonic foraminifera assemblages continued to change into the current warm period for several thousand years, post-dating the last deglaciation, even though temperature forcing during this time period was comparably low (Figure 3-2). The observation of asymmetric range shifts (Figure 3-3) and the emergence of novel assemblages in the mid-latitudes during the current warm period (Figure 3-4), raises the question about the role of ecological forcing during periods of relatively low temperature forcing. Consequently, the observed discrepancy between assemblage change and SST during the current warm period leads to the rejection of the first hypothesis (H1). Particularly during time periods of relatively stable environmental conditions, such as the Holocene, planktonic foraminifera did not exhibit equilibrium with SST change.

Moreover, this thesis provides a refined temporal perspective on the emergence of a tropical diversity decline between the last cold stage and pre-industrial times reported by Yasuhara et al. (2020b). Although in this thesis no change in tropical species richness is observed, the Shannon diversity at low latitudes progressively declined with the end of the last deglaciation at around 12 ka ago (Figure 3-5d). This decline first led to the flattening of the LDG during the beginning of the Holocene and eventually resulted in the development of the tropical diversity dip in the late Holocene (Figure 3-5c).

### H2: The response of phytoplankton and zooplankton to SST change is comparable

Comparing the planktonic foraminifera response with other functional groups of marine plankton revealed that comparable responses of planktonic foraminifera, coccolithophores and dinoflagellates cysts to past climate change during the past 24 kyr. Assemblage change in all plankton groups began with the onset of global warming around 16 to 17 ka ago and persisted until 4 to 5 ka ago, exhibiting similar time periods of significant change (Figure 4-3). Additionally, all plankton groups showed comparable patterns in local rates of biodiversity change (Figure 4-5) and spatio-temporal evolution of species alpha-diversity during the past 24 kyr (Figure 4-6), supporting the acceptance of the second hypothesis (H2) that phytoplankton and zooplankton responses to past climate change are similar. The observed discrepancies in assemblage change among different functional groups of marine plankton during the current warm period further strengthens the question about the role of ecological forcing during periods of relatively low temperature forcing.

### H3: Local SST change explains more variance in planktonic foraminifera assemblage change than global SST

Contrary to our initial expectation, the comparison of local planktonic foraminifera assemblage changes with local and global SST change during the current warm period revealed that global SST explains more variance in local planktonic foraminifera change than local SST (Figure 5-4) and there is significant evidence to reject our third hypothesis (H3). This unexpected finding raises puzzling questions, as planktonic foraminifera are presumed to respond more directly to temperature changes in their local environment rather than global SST. Additionally, there is notable discrepancy between the observed assemblages changes in planktonic foraminifera during the current warm period and the local SST variations (Figure 5-5a,b and Figure 5-6), along with a different latitudinal pattern in the partitioning of change (Figure 5-5c,d). These contradictions challenge our initial assumption that assemblage change and SST change should be positively correlated, given the species composition of planktonic foraminifera is mainly affected by SST changes (Morey et al., 2005; Rillo et al., 2021).

Effects of age uncertainty, temporal resolution, spatial homogenisation, and other environmental and ecological factors have been considered and ruled out as potential explanations for the differences between local and global SST reconstructions. These findings raise cautionary flags regarding the application and interpretation of SST reconstructions from global climate models, as they may not accurately reflect realistic SST variations during time periods with relatively low temperature change, such as the current warm period.

## 7.2 Assessing the impact of multiple drivers of marine plankton assemblage change

This thesis focuses on the marine plankton response to climate change, where SST serves as a key predictor for species composition of planktonic foraminifera, coccolithophores and dinoflagellates. However, marine plankton groups do not exist in isolation in the marine realm, in fact, numerous biotic interactions with other marine organisms (e.g., grazing pressure, food availability, endosymbiont fitness, exposure to pathogens, parasites) contribute to the complex dynamics and feedback mechanisms of marine ecosystems, showing that environmental factors alone are insufficient to predict plankton community structure (Lima-Mendez et al., 2015).

In this thesis, the observed plankton response in the North Atlantic Ocean during the current warm period does not entirely align with SST (Figure 4-3; Figure 5-1), indicating a possible change of the relationship between planktonic foraminifera and SST within the past 24 kyr (Figure 5-10). Furthermore, the emergence of novel assemblages in the mid-latitudes of the North Atlantic Ocean with the beginning of the current warm period (Figure 3-4) caused by the asymmetrical poleward range shifts (Figure 3-1b; Figure 4-5) indicate new direct and indirect ecological interactions between plankton groups in the Holocene compared to the last deglaciation. One explanation for these results might be a dominance shift in the drivers of plankton assemblage change from more environmental-dominated factors during the last deglaciation to more ecological-dominated factors under reduced environmental forcing during the current warm period. Assessing the impact of non-climatic drivers (e.g., ecological interactions) and their relative contribution to plankton assemblage through time will be crucial for the prediction of marine plankton assemblage change to expected future global warming.

To assess this shift, the use of the index of relative entropy of community assembly (RECA), recently developed by Doncaster et al. (2023), could be applied to the data in this thesis. The RECA index measures the relationship between disorder (the degree of randomness in species composition change through time) and alpha-diversity in a time series of species composition data. A positive correlation between disorder and alpha-diversity suggests more unpredictable changes in the community, driven by external drivers such as environmental forcing. On the other hand, a negative correlation indicates more ordered changes (i.e., internal drivers), where species entering the community have a higher chance to stay in, and species exiting the community having a higher chance to stay out. Doncaster et al. (2023) observed a shift in the dominant drivers of terrestrial plant species composition from abiotic forcing (i.e., temperature) to biotic forcing (i.e., niche construction, competition) at around 9 ka, showing that RECA can be used to identify changes in the dominant drivers of species composition over time. Understanding potential shifts in these drivers will improve predictions of the plankton response to future climate change. For instance, model inputs could be refined by accounting for the different drivers of species composition and dynamics leading to more realistic model projections of how marine plankton may respond to future climate change. Moreover, identifying time periods when marine plankton species were particularly sensitive to environmental changes can help to predict potential sensitivity periods in the future which will be important for future conversation strategies.

Even though anthropogenic climate change is the biggest threat to the marine realm (IPCC, 2023), it also faces threats beyond future anthropogenic climate change, namely various non-climatic natural and anthropogenic stressors. Particularly human-induced stressors, such as pollution, invasive species introduction through shipping, overexploitation, habitat destruction, and excessive nutrient run-off from agriculture or sewage discharge, pose significant threats (Maxwell et al., 2016), leaving no area of marine ecosystems unaffected (Halpern et al., 2008). In fact, marine biodiversity is often affected by a multitude of climatic and non-climatic stressors with different interactive effects. These stressors can affect the performance of marine plankton without interaction (additive stressors), but they can also interact by dampening or amplifying the individual effects on the performance, leading to non-linear and unpredictable responses of the plankton (Todgham and Stillman, 2013). Furthermore, these stressors impact marine plankton on many different ecological scales including the physiological, individual, population, community, and ecosystem level with changing relative importance at each scale (Simmons et al., 2021). For instance, extreme temperature may lead to the death of individual plankton specimens, resulting in the decrease of species abundance on the population level and to a potential loss of species on the community level. On the marine ecosystem level these extreme temperatures might lead to decreased productivity of plankton groups and an overall loss of biomass with potential implications for the whole trophic web.

Consequently, understanding and addressing these multiple stressors and their feedback mechanisms is essential for marine plankton population conservation and overall health of marine ecosystems. In recent years, multiple-stressor research has gained traction, but is often still limited by the consideration of only few non-interacting stressors or few ecological scales (Simmons et al., 2021). A further lack of standardised terminology across different disciplines hinders cross-disciplinary unified approaches (Orr et al., 2020). Nonetheless, to safeguard marine biodiversity and the marine realm as a whole, a collective effort through international collaborations and a multi-faceted approach involving cross-disciplinary scientific research, science-informed policy development and public awareness is needed (Ward et al., 2022).

## 7.3 The challenge of accelerated future climate change

The transition from the last cold stage to the current warm period (i.e., past 24 kyr) is an ideal time period to study the plankton response to SST changes. The magnitude of environmental change during this period is comparable to the predicted future changes (Figure 1-3), therefore, providing valuable insights into the pre-anthropogenic baseline, long-term effects and the natural variability of marine plankton change. However, it is essential to note that while the magnitude of environmental change is comparable, the rate of change is significantly different. The main temperature change of the last deglaciation occurred over a time period of several thousands of years (approximately 10-17 ka), whereas a similar temperature change is predicted to occur within the next century (Figure 1-3; IPCC, 2023). This predicted accelerated rate of future change has several implications on the future response of marine plankton.

To avoid extinction, marine plankton can respond to climate change through geographical range shifts, changes in phenology, or adaptation to the new conditions (Munday et al., 2013; Poloczanska et al., 2013). Asymmetric geographic range shifts (Figure 4-5), caused by the poleward migration of species and the persistence of the original species in these habitats (Figure 4-6), has led to the formation of novel assemblages in the mid-latitudes during the past 24 kyr (Figure 3-4). The persistence of these original species in the mid-latitudes, where the range of seasonal temperature is greater than in tropical and polar regions (Figure 7-1), might indicate that they have evolved the capacity to deal with the temperature changes that occurred during the past 24 kyr (Somero, 2005; Munday et al., 2013). The predicted SST increase until 2100 will most likely exceed the seasonal SST range in many areas of the marine realm except the mid-latitudes, posing a severe threat on marine organisms that live in the uppermost surface water layers such as many plankton species. Another question remains, whether the rapid rate at which future warming is predicted to happen (Figure 1-3; IPCC, 2023) may potentially outpace the ability of marine plankton to respond through range shifts or exceed their thermal plasticity.

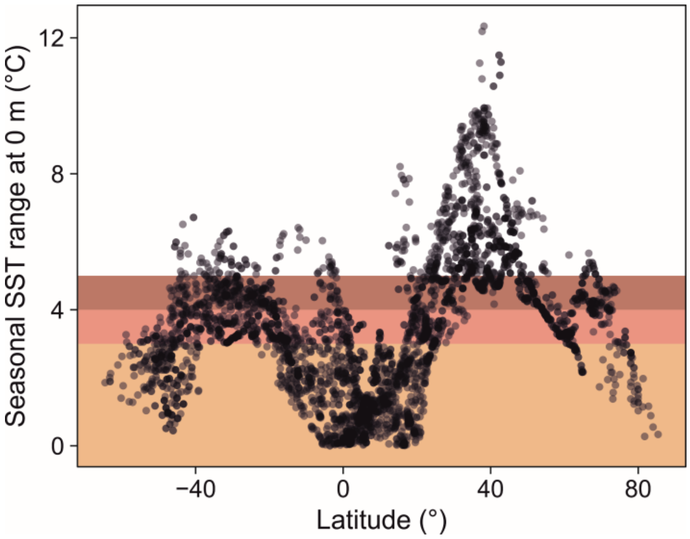


**Figure 7-1:** Seasonal sea surface temperature (SST) range calculated as the difference between winter and summer SST at 0 m water depth for all ForCenS calibration dataset samples (Siccha and Kucera, 2017). Future warming scenarios representing a warming until 2100 of 3°C, 4°C, and more than 4°C since the onset of the industrialisation are indicated as background shadings (orange, red and dark red, ICPP, 2023). Temperatures are from the World Ocean Atlas 1998 (Levitus and US National Oceanographic Data Center, 2012).

Already, modern plankton is affected by anthropogenic climate change (Jonkers et al., 2019) and the decline of tropical diversity in marine plankton is detectable (Figure 4-6; (Yasuhara et al., 2020b). Therefore, rapid future warming may cause severe species losses in the tropics with no source of potential immigrants (Beaugrand et al., 2015; García Molinos et al., 2016; Yasuhara et al., 2020b). Moreover, polar regions may not necessarily experience a net loss of species through the migration of warm-adapted species, but cold-adapted species may lose their habitats and perish under ongoing global warming (García Molinos et al., 2016; Yasuhara and Deutsch, 2022). Consequently, a better understanding of the potential impacts of accelerated climate change on the marine plankton response and its interplay with other anthropogenic and natural pressures is essential for policy development and effective conservation efforts for the marine realm. For instance, this thesis revealed how paleo data can help with the establishment of a pre-anthropogenic baseline and the identification of plankton communities that have demonstrated resilience to past climate change. Plankton species in the mid-latitudes coped with the SST change during the past 24 kyr (Figure 4-6), potentially due to the high seasonal SST range in these regions (4-10 °C; Figure 7-1). As this SST range is comparable with predicted future warming (Figure 1-3; IPCC, 2023), plankton species from mid-latitudes might be more capable to cope with the expected future warming until 2100 of up to over 4 °C (IPCC, 2023) since the last industrialisation than polar and tropical species.

# 8

# Conclusion

By analysing the spatio-temporal patterns of marine plankton biodiversity change in the North Atlantic Ocean across the transition from the last ice age to the current warm period, this doctoral thesis aimed to assess the long-term response of marine plankton to climate change that is comparable in its magnitude to predicted future global warming. It can be concluded that the response of marine plankton to SST might not be as straightforward as previously assumed, which is quite surprising, given that the modern species composition of many marine plankton groups is mainly affected by changes in SST. This thesis showed that the response of marine plankton from different functional groups to climate change was not always at equilibrium since the last ice age, raising the question about the role of ecological forcing and other environmental factors during periods of relatively low temperature forcing, while also revealing that SST reconstructions from global climate models may not accurately reflect realistic SST variations during these periods.

Validating and evaluating the accuracy of SST reconstructions, whether derived from proxies or models, will be essential in understanding past biodiversity dynamics. The reliability of SST estimates can be assessed using a multi-faceted approach. Comparisons with independent proxies, such as foraminiferal Mg/Ca ratios, alkenone biomarkers, or oxygen isotopes, enable cross-validation and provides insights into the plausibility of inferred temperature changes while also circumventing age issues that may appear when using SST reconstructions from climate models. Additionally, evaluating the sensitivity and response time of several proxy methods against known climatic events, such as the transition from the last ice age to the current warm period, will help in assessing the proxies' ability to capture real changes in SST and disentangle potential carrier specific and non-climatic influences on proxies. Furthermore, comparing SST reconstructions from different proxies and models allows for uncertainty estimation and identification of potential biases. Consequently, assessing the spatial and temporal congruence between reconstructed SST and observed biodiversity changes in sedimentary records can provide a comprehensive perspective on the link between climate and biodiversity dynamics, ultimately enhancing the confidence in using SST reconstructions to evaluate past biodiversity responses to climate change.

This thesis revealed how paleo data can help to establish the pre-anthropogenic baseline, which will be essential for aiding predictions of the plankton response to future anthropogenic climate change. Furthermore, it showed how continuous spatio-temporal cross-scale analyses can help to identify plankton communities that have demonstrated resilience or sensitivity to past climate change, which will be important for future conservation strategies. However, the current marine realm is not only threatened by anthropogenic climate change, but by a multitude of human-induced stressors. Understanding the impact of these stressors and their complex feedback mechanisms will be crucial for the conservation and overall health of the marine realm. Models that predict possible biodiversity responses to climate change should account for these different stressors and their feedback mechanisms as well as integrate insights obtained from the fossil record. While many advances in multi-stressor research have recently been made (Simmons et al., 2021), cross-disciplinary unified approaches are still hindered by a lack of standardised terminology across the different disciplines (Orr et al., 2020).

The overall progress of (paleo)climate and micropalaeontological research is closely tied to the standardisation of scientific data and while much work has been done to increase the standardisation and FAIRness of scientific data in recent years (e.g., Wieczorek et al., 2012; Wilkinson et al., 2016; Khider et al., 2019; Jonkers et al., 2020), this thesis particularly highlights the lack of standardisation of micropaleontological data. While demonstrating the potential of paleo data to unravel the long-term response of marine plankton to past climate change, it also clearly shows that these kinds of spatio-temporal studies are limited by a lack of (meta)data guidelines for microfossil assemblage data. Increasing the reusability and interoperability of new and already existing datasets, will help to unlock the full potential of paleoecological data for global analyses, to better understand and predict the impact future global change will have on the marine realm.

In conclusion, a better comprehension of the potential impacts of accelerated climate change on marine organisms and its interplay with other anthropogenic pressures will be essential to safeguard marine biodiversity and the marine realm as a whole. For this, a collective effort through international collaborations and a multi-faceted approach involving cross-disciplinary scientific research, science-informed policy development and public awareness is needed. This need for such unified international effort becomes even more important considering that the vast majority of the marine realm is beyond national jurisdiction.

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