Evolutionary dynamics of Cenozoic planktonic foraminifera: insights from biogeography, geochemistry, and morphology

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The candidate confirms that the work submitted is his own, except where work which has formed part of jointly authored publications has been included. The contribution of the candidate and the other authors to this work has been explicitly indicated below. The candidate confirms that appropriate credit has been given within the thesis where reference has been made to the work of others.

The work in Chapter 2 of the thesis has appeared in publication as follows:

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I was responsible for designing the project, collecting the raw datasets, downloading, and formatting age models, and drafting the manuscript.

The contribution of the other authors was designing the project, collecting raw datasets, coding the database, advice on taxonomy, age models, and databases, drafting the manuscript, and comments/feedback.

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I was responsible for designing the project, generating, and interpreting the primary data, coding for statistical analysis, figure creation, and drafting the manuscript.

The contribution of other authors was generating and interpreting the primary data, drafting the manuscript, and comments/feedback.

plankton – from the Ancient Greek “πλαγκτός”, meaning “wanderer” or “drifter”. Coined by Christian Andreas Victor Hensen in 1887.

“The case of the 3 species of Protozoon (I forget the name) which apparently select differently sized grains of sand & is almost the wonderful fact I ever heard of. One cannot believe that they have mental power enough to do so, & how any structure or kind of viscidity can lead to this result passes all understanding.”

- Charles Darwin

“To see a World in a Grain of Sand…”

- William Blake

“Your answers were always lying on the ocean bed…”

- Roughton Reynolds

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My childhood obsession with palaeontology and extinction really came to fruition during my undergraduate studies upon discovering Paul’s fantastic work with Prof Anthony Hallam “Mass Extinctions and Their Aftermath”, which has not left my bookshelf ever since. Paul’s unmatched knowledge and guidance on the fossil record and extinction has inspired me since day one of my academic journey and continues to do so as I look towards the future.

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Abstract

The Earth is currently experiencing rates of environmental change unprecedented in the last 66 million years. As climate change accelerates, the need to quantify biotic responses associated with heightened extinction risk is becoming more urgent. The fossil record can provide a rich source of information about biotic responses to past environmental perturbations that can help ground truth predictions about future biodiversity responses. The marine microfossil record represents the most-complete biological archive available for this kind of study, with the macroperforate planktonic foraminifera having the most complete species-level fossil record of the last 66 million years. These organisms have a globally distributed fossil record and their readily fossilized calcium carbonate skeletons preserve a biogeochemical fingerprint of the environments in which they lived, as well as their ecological habits.

This thesis builds on this exceptional fossil record, first and foremost by assembling a new Cenozoic fossil occurrence database, Triton, the largest group specific fossil occurrence dataset ever created with 512,922 individual planktonic foraminiferal records.

Using Triton, the pre-extinction geographic range trajectories of Cenozoic planktonic foraminifera were largely demonstrated to show a reduction in geographic range prior to extinction. However, multiple taxa which speciate in the upper water column, and host photosynthetic algal symbionts exhibit pre-extinction range expansion, potentially indicating ecological resilience to selection pressures. Amongst significant climatic events through the Cenozoic, the Paleocene-Eocene Thermal Maximum (56 Ma) impacted pre-extinction geographic ranges most significantly, despite the muted effect of this event on planktonic foraminiferal species richness.

The investigation of the palaeolatitudinal dynamics of speciation and extinction shows that Cenozoic global temperatures are the primary control on the palaeolatitude of speciation, where a warmer world is typified by a greater proportion of speciation taking place at higher palaeolatitudes. Furthermore, speciation locations tend to be geographically isolated, despite the interconnectivity of the pelagic ecosystem, and the majority of species exhibit an extinction palaeolatitude removed from their palaeolatitude of speciation.

Finally, high-resolution morphological, and geochemical examination of the planktonic foraminiferal record revealed a suite of pre-extinction responses during the extinction of two members of the genus *Dentoglobigerina*. Despite phylogenetic, morphological, and ecological affinity, these taxa exhibit species-specific phenotypic modifications which include permanent depth migration, “pre-extinction gigantism”, and photosymbiont bleaching.

The results generated through the construction of Triton, and high-resolution examination of the extinction of species of *Dentoglobigerina*, reveal a variety of spatiotemporal evolutionary dynamics with implications for improving our understanding of the nature of evolution within the largest ecosystem on Earth.

Contents

1. Introduction

The Earth is presently undergoing the most severe climatic and biotic rates of change recorded in 66 million years (Myrs). Investigations of modern biodiversity show heightened extinction risk and population shifts within both the marine and terrestrial realms (Pinksy et al. 2018; Jonkers et al. 2019) as the oceans and atmosphere advance towards conditions not witnessed since pre-human times (Figure 1).

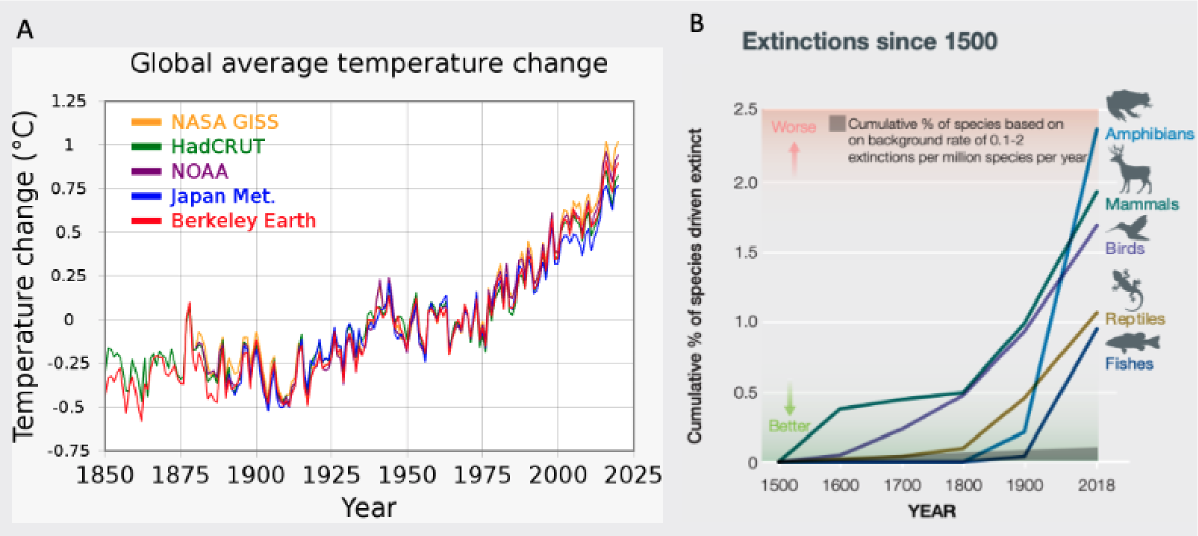

Figure 1. A) Graphs showing correlation of measured global average temperature from 1850 – 2021, from five different scientific organizations: NASA, NOAA, Berkeley Earth, and meteorological offices of the U.K. and Japan. The data show substantial agreement concerning the progress and extent of global warming: pairwise correlations range from 98.09% to 99.04%. Source: Wikipedia. B) Extinctions since 1500 for vertebrate groups. Rates for reptiles and fishes have not been assessed for all species. Source: IPBES (2019).

The most conservative estimates infer that current extinction rates are at least eight times higher than the Cenozoic background average, leading to the commonplace reference to a modern day “sixth mass extinction” (Barnosky et al. 2011; Kolbert 2014; Ceballos et al. 2015). Despite conservation efforts, extinction rates continue to rise at a geologically unprecedented rate due to both human activities and anthropogenically-driven climate change, leading to a potential loss of anywhere from 2.8-16% of modern species by 2100 (IPCC, 2014; Urban, 2015). As such, there a pressing need to better understand and predict extinction risk in modern ecosystems. Fundamental differences exist between the primary datasets used to forecast ancient and modern extinction rates; the former are often multi-million-year scale marine records, and the latter typically decadal to centennial modern terrestrial records (Hull et al. 2015). Consequently, the modern marine realm is comparatively understudied (Spalding et al. 2008; Cox et al. 2016), making predictions on the response of marine organisms to rapid climate change incredibly challenging. As a considerable proportion of the human population rely heavily upon marine life as a primary source of nutrition and for economic gain (Bindoff et al. 2019), it is imperative that the fundamental processes governing marine biodiversity are better understood to better identify extinction risk and aid conservation efforts required to support a sustainable future (https://sdgs.un.org/goals; Jenkins et al. 2013; Halley et al. 2018; Pinksy et al. 2018; Cantalapiedra et al. 2019; Tucker et al. 2019; Chenillat et al. 2021).

Marine plankton ecological and population dynamics influence the entire trophic structure of the ocean, however the lack of geologically preservable structures within many plankton groups (Sáez et al. 2004; Boere et al. 2011) limits their utility for understanding marine ecosystem changes through deep time. Of all marine microplankton groups which produce preservable skeletons, the macroperforate planktonic foraminifera are considered to exhibit the most well-resolved fossil and ecological history (Aze et al. 2011; Ezard et al. 2011), and in spite of a lack of known selective predators (Schiebel & Hemleben, 2017), due to cosmopolitan species distributions and high concentrations within the marine sedimentological record the group represent the most-comprehensive biological archive for basal marine trophic levels from the last 66 million years (Aze et al. 2011).

In this thesis, the exceptional marine macroperforate planktonic foraminiferal record is used to study Cenozoic evolutionary dynamics with a particular focus on abiotic drivers and biotic responses, and how they may improve our understanding of biodiversity dynamics in the marine realm.

1.1 Planktonic foraminifera

1.1.1 Biology & ecology

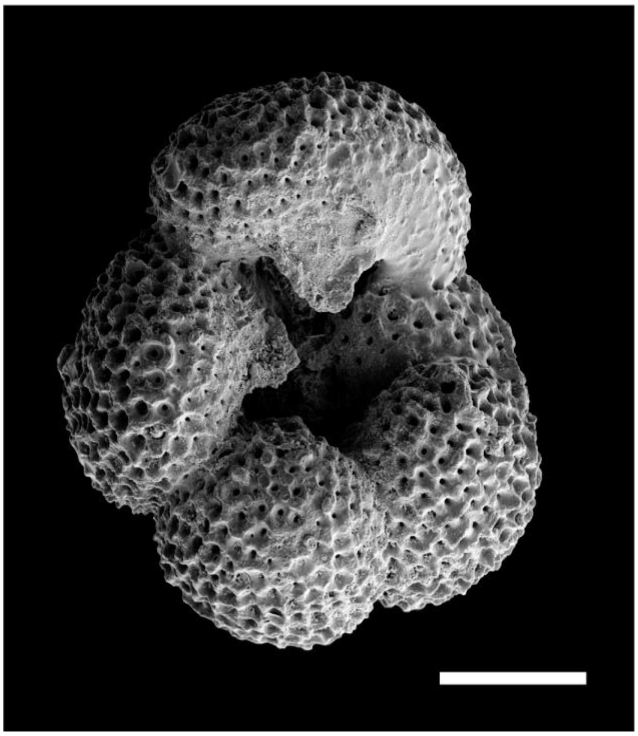

Figure 2. Scanning electron microscope image of the calcareous test of the extinct species *Dentoglobigerina altispira*. Specimen from the east equatorial Pacific Ocean, ~3 Myrs old. Scale bar = 100 µm.

Planktonic foraminifera are single-celled marine protozoans that produce a biomineralized multi-chambered calcium carbonate skeleton or "test" (Figure 2). Modern species are found globally from tropical to polar latitudes, exhibiting their greatest absolute abundances and diversity within the lower latitude surface mixed layer of the water column (0-100 mbsl) (Rutherford et al. 1999; Roy et al. 2015; Fenton et al. 2016a; Schiebel & Hemleben, 2017). Their reproduction and life cycle are primarily associated with dwelling depth, where shallow water taxa (0-400 mbsl) follow the synodic lunar cycle, whilst deeper dwellers (recorded down to 2000 mbsl) appear to reproduce annually (Hemleben et al. 1989; Schiebel & Hemleben, 2005, 2017). Distinctive morphological and ecological classes (Aze et al. 2011) exhibit specialization to different niche and living/reproductive depth strategies dependent on individual species nutritional and life requirements e.g., water temperature, salinity, radiation, turbidity, abundance of prey, trophic demands (Schiebel & Hemleben, 2017; Schiebel et al. 2018). Moreover, many species that occupy the euphotic zone are observed to host a whole spectrum of relationships with photosymbiotic algae hailing from a variety of different clades (Figure 3) (Hemleben et al. 1989; Schiebel & Hemleben, 2017; Takagi et al. 2019).

Throughout species ontogeny, test calcification preserves a biogeochemical expression of the surrounding water column which is dependent upon physicochemical changes associated with depth (Emiliani, 1954; Aze et al. 2011; Birch et al. 2013; Edgar et al. 2017), metabolically-driven isotopic fractionation (Spero & Dinero, 1987; Ravelo & Fairbanks, 1992, 1995; Spero, 1992; Spero & Lea, 1993, 1996; Spero et al. 1997; Birch et al. 2013), and global-scale trends in marine stable isotope and trace elements pools (Emiliani, 1955; Shackleton, 1967; Cramer et al. 2009; 2011; Lécuyer, 2016; Schiebel & Hemleben, 2017). These features allow for the reconstruction of the life habits of modern and extinct planktonic foraminiferal species (Birch et al. 2013), and despite a susceptibility to diagenetic overprinting and secondary calcification (Pearson et al. 2001; Sexton et al. 2006; Edgar et al. 2015), due to their excellent preservation potential and high abundance within the marine sedimentological record, the fossil and geochemical records of planktonic foraminifera have been applied extensively to furthering our understanding of ancient and recent changes in Earth’s climate.

1.1.2 Biogeography & provinciality

The quantification of modern and late Quaternary planktonic foraminiferal biogeography and provinciality has been made possible through significant plankton tow, sediment trap, and shallow coring efforts (Brady, 1884; Bé, 1962, 1977; Bé & Tolderlund, 1971; Be & Hutson, 1977; Bé et al. 1977, 1985; Deuser et al. 1981; Hemleben et al. 1989; Prell et al. 1999; Spencer-Cervato, 1999; Diepenbroek et al. 2002; Reid et al. 2003; Schiebel & Hemleben, 2005, 2017; Žarić et al. 2005; Sellén et al. 2010; O’Regan, 2011; de Vargas et al. 2015; Van Sebille et al. 2015; Siccha & Kučera 2017; Takahashi et al. 2017; Schiebel et al. 2018; Waelbroeck et al. 2019). Modern species can be largely subdivided into a succession of latitudinally assorted provincial assemblages which exhibit a bimodal diversity peak in the lower latitudes (Figure 4) defined mainly by sea surface temperature (Rutherford et al. 1999; Fenton et al. 2016a; Schiebel et al. 2018). Deep-time sedimentary archives for biogeographical analyses are comparatively limited to the records in the Recent, however, onshore records have been considerably complimented by deep-ocean datasets following the advent of scientific ocean drilling (Bascom, 1961; Winterer, 2000; National Research Council, 2011; Becker et al. 2019).

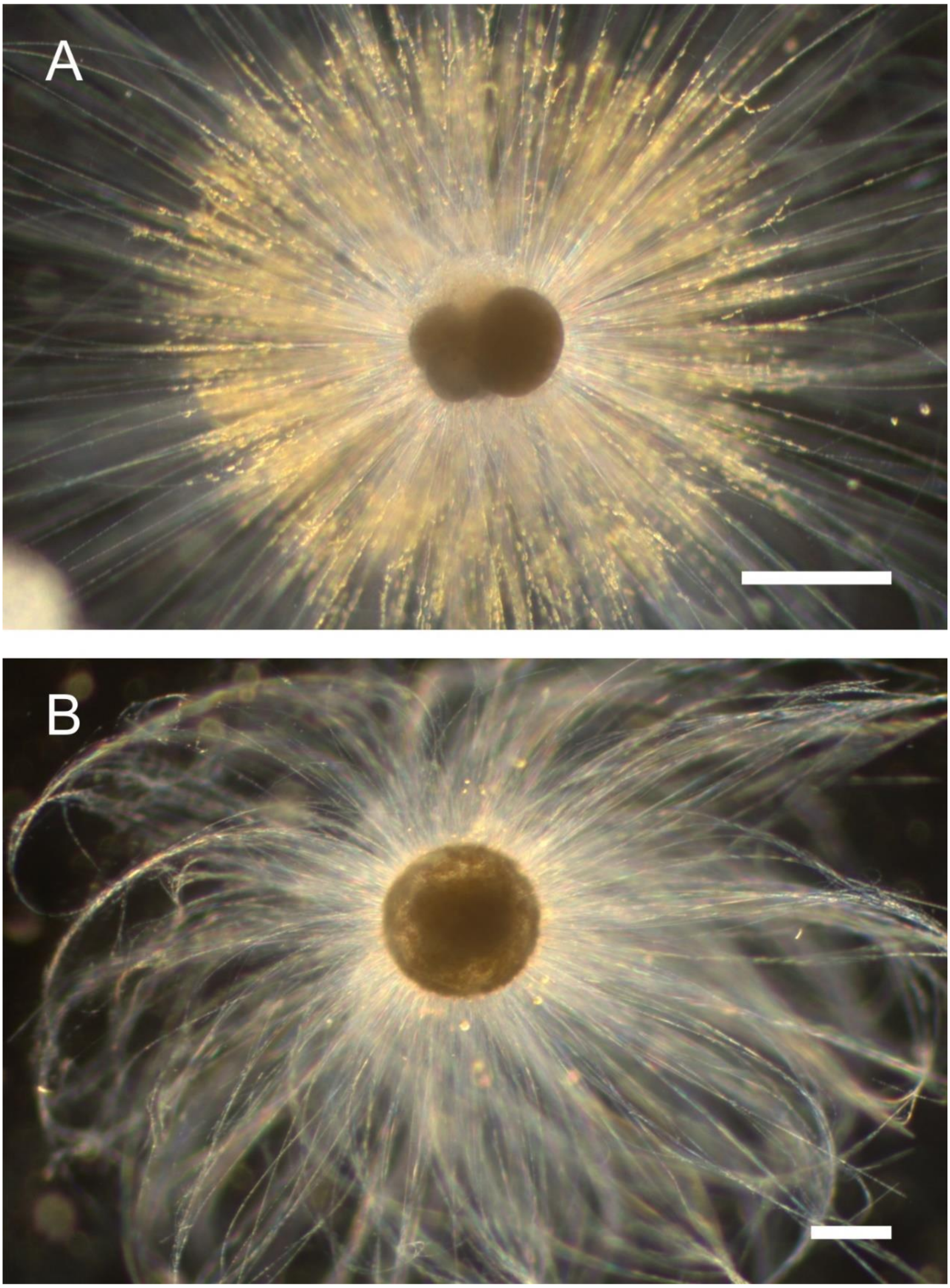

Figure 3. Living specimens of A, juvenile and B, adult, *Orbulina universa* from offshore California illustrating the variability of density in the external expression of photosymbiotic algae (light yellow objects) housed by planktonic foraminifera. Credit – Prof Howie Spero. Scale bar = 300 µm.

1.1.3 Cenozoic fossil record, diversity, and climate

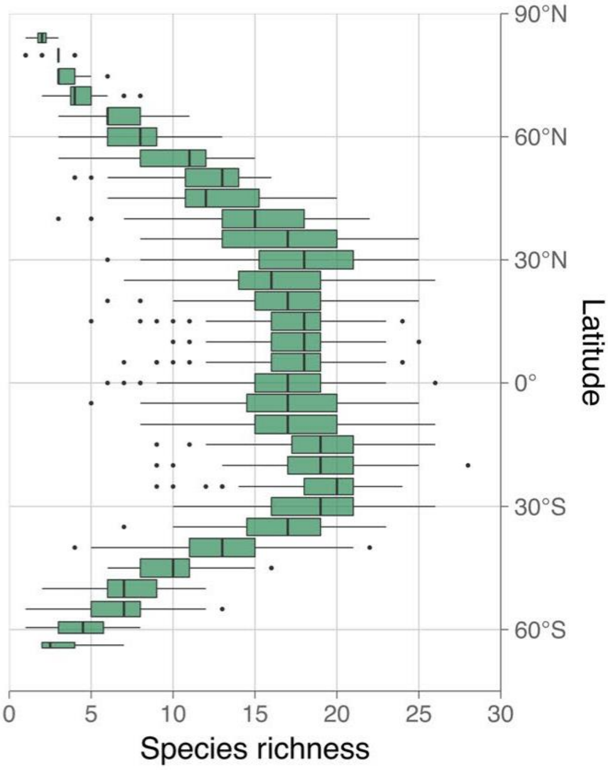

Figure 4. Latitudinal species richness of modern planktonic foraminifera binned to 5° latitudinal bands based on coretop data. From Rillo et al. (2019).

The Cenozoic planktonic foraminiferal fossil record represents the most-complete and robust species-level data archive available to science (Aze et al. 2011). The compilation of planktonic foraminifera fossil occurrences initially grew from a necessity to find reliable index fossils for Cenozoic stratigraphic correlation following the demise of the ammonites at the Cretaceous-Paleogene (K-Pg) mass extinction event (Cushman, 1925; Loeblich & Tappan, 1957a; Bandy, 1964; Blow, 1966). Work on the revision of the Cenozoic timescale has continued throughout the 20th-century and through examination of outcrop data (e.g. Bandy, 1964; Bolli & Bermudez, 1965; Bolli, 1966; Blow, 1969) and deep-sea drilling program marine sediments (Berggren, 1969a, b), knowledge of the group's evolutionary and biogeographic history within the context Cenozoic climate development has been significantly advanced (Figure 5) (e.g., Douglas & Savin, 1978; Keller, 1985; Shackleton et al. 1985; Boersma et al. 1987; Collins, 1989; Hornibrook et al. 1989; Jenkins, 1992a; Pearson et al. 1993; D'Hondt et al. 1994; Pearson, 1998a, b, c; Norris, 1996; 1999, 2000; Coxall et al. 2000; Pearson et al. 2001; Quillévéré et al. 2001; Schmidt et al. 2004a, b; 2006; Ravelo & Hillaire-Marcel, 2007; Wade et al. 2008; Wade & Olsson, 2009; Pearson, 2012; Birch et al. 2013; Aze et al. 2014; Edgar et al. 2017; Brombacher et al. 2017).

The Cenozoic planktonic foraminifera are subdivided into three distinct groups based upon the texture and ultrastructure of their calcareous skeletons: microperforate, medioperforate, and macroperforate (Pearson, 2018). The phylogenetic history and fossil record of the two former groups is less well represented (Figure 6) and they are comparatively understudied, though their planktonic lifestyle appears to stem from convergent evolution through multiple currently indeterminate benthic ancestors (Li & Radford, 1991; Darling et al. 1996, 1997; Wade et al. 1996; de Vargas et al. 1997; Pearson 2018). The Cenozoic macroperforate planktonic foraminifera, however, represent a monophyletic clade descended from the Late Cretaceous species, *Muricohedbergella holmdelensis* that survived the K-Pg

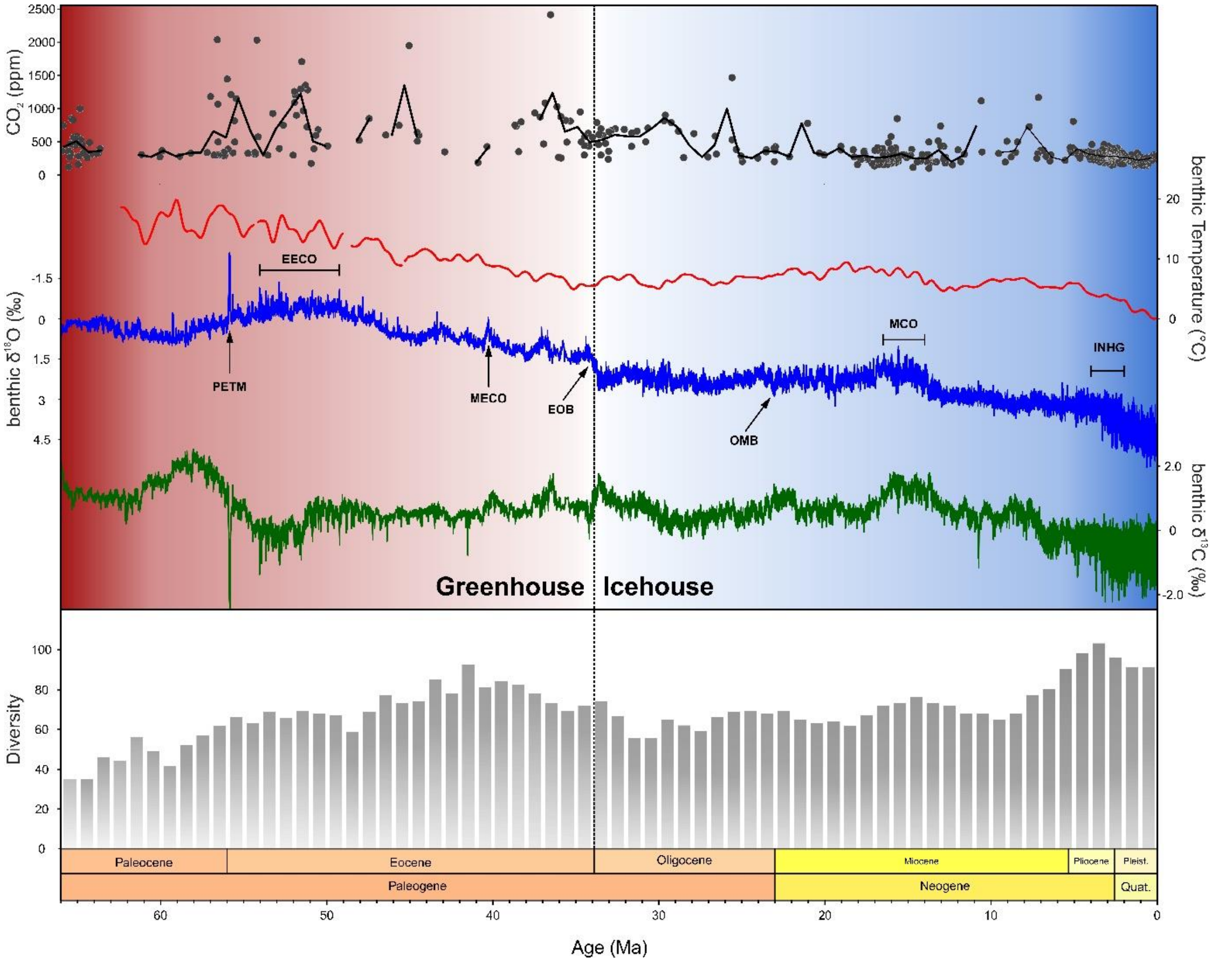

Figure 5. Cenozoic compilation of Triton (Fenton & Woodhouse et al. 2021) planktonic foraminiferal morphospecies diversity, abiotic climate parameters, and major climate events. Benthic foraminiferal δ^{13}C and δ^{18}O from Westerhold et al. (2020), atmospheric CO$_2$ data from Foster et al. (2017) and Rae et al. 2021; benthic (Mg/Ca) temperature from Cramer et al. (2011). PETM = Paleocene-Eocene Thermal Maximum, EECO = Early Eocene Climatic Optimum, MECO = Middle Eocene Climatic Optimum, EOB = Eocene-Oligocene Boundary, OMB = Oligocene-Miocene Boundary, MCO = Miocene Climatic Optimum, INHG = Intensification of Northern Hemisphere Glaciation.

event (Olsson et al. 1999; Aze et al. 2011; Fraass et al. 2015; Lowery & Fraass, 2019; Lamyman et al. in prep.). In the aftermath of the extinction, gradual reconstruction of ecological niche complexity took place amongst species across the first 10 Myrs of the Cenozoic (Lowery & Fraass, 2019). Across this interval, the Earth progressively warmed, exhibiting a series of geologically transient "hyperthermals", most notably of which, the Palaeocene-Eocene Thermal Maximum (PETM) (Figure 5), which resulted in the extinction of ~50% of all benthic foraminiferal calcifiers (Thomas, 1989; Thomas & Monechi, 2007; Schmidt et al. 2018). Biodiversity amongst calcareous plankton does not reflect this loss, rather, ecological responses are consistent with the occurrence of thermally prohibitive tropical marine temperatures (Huber, 2008; Tewksbury et al. 2008; Bown & Pearson, 2009; Speijer et al. 2012; Aze et al. 2014; Frieling et al. 2017, 2018; Si & Aubry, 2018; Shaw et al. 2021) and higher rates of turnover (Figure 5) (Kelly et al. 1998; Gibbs et al. 2006; Aze et al. 2011; Speijer et al. 2012; Edgar et al. 2013a; Fraass et al. 2015; Alvarez et al. 2019; Lowery & Fraass, 2019; Lowery et al. 2020).

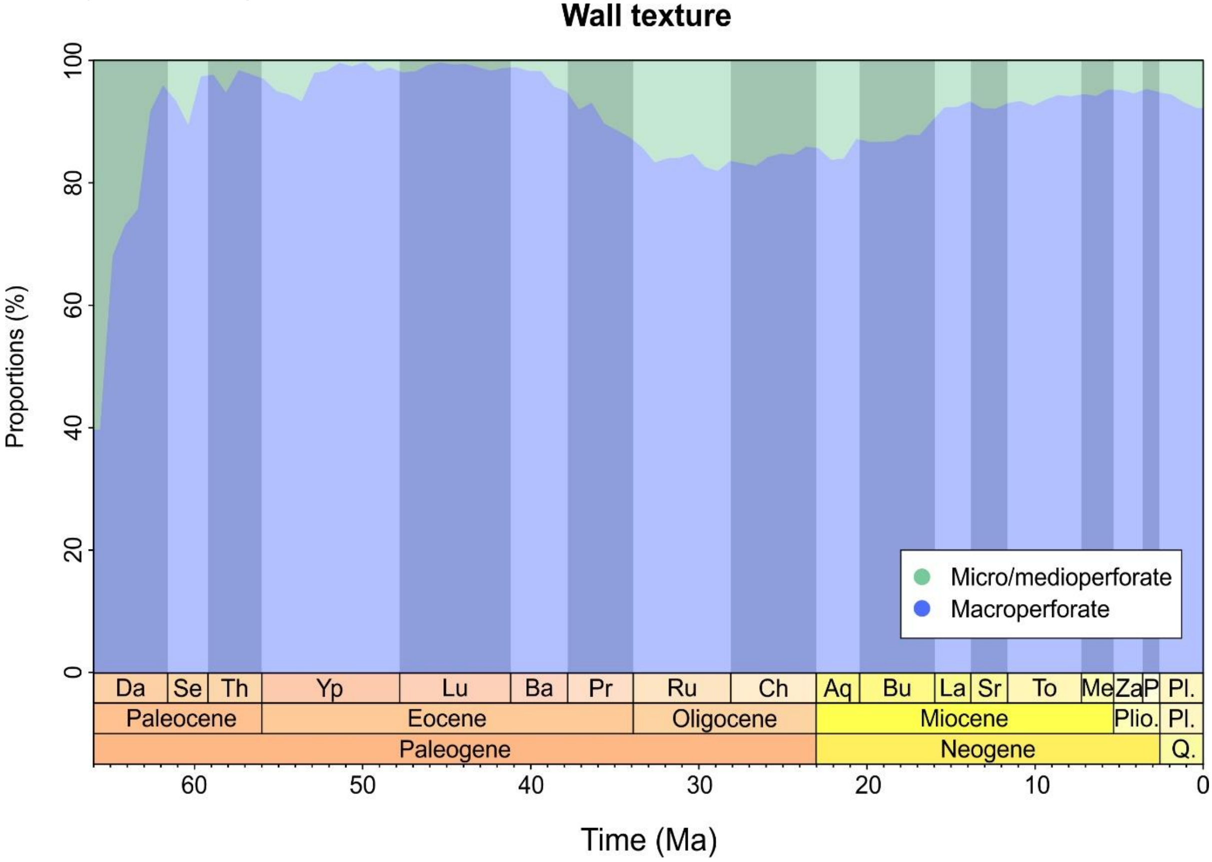

Figure 6. Proportions of planktonic foraminiferal occurrences within Triton based upon wall texture of species.

Global warmth peaked at ~50 Ma during the Early Eocene Climatic Optimum (Figure 5) (EECO), after which decreasing global temperatures marked the commencement of the “Descent in the Icehouse”, a long-term deep sea cooling trend which typifies the remainder of the Cenozoic (Figure 5) (Pearson et al. 2001; Zachos et al. 2001; Thomas, 2008; Liu et al. 2009; Pross et al. 2012; Hyland & Sheldon, 2013; Passchier et al. 2013; Inglis et al. 2015; Holbourn et al. 2015; Anagnostou et al. 2016; Westerhold et al. 2020; Hutchinson et al. 2021). Post-EECO, diversification rates amongst the macroperforate planktonic foraminifera were at their highest and species richness was at a maximum since the K-Pg just prior to the initiation of the Middle Eocene Climatic Optimum (MECO, ~40 Ma), a transient period of global warming which interrupted the overall trend of Cenozoic temperature decline (Figure 5) (Haq et al. 1977; Thomas, 2008; Boscolo-Galazzo et al. 2014; Henehan et al. 2020; Westerhold et al. 2020). As the post-ECCO cooling was established, global marine palaeoceanography was characterised by a significant strengthening of latitudinal sea-surface temperature (SST) gradients, coeval with extinction of larger, ornate Paleogene macroperforate forms such as *Acarinina, Morozovella,* and *Morozovelloides* (Wade, 2004; Aze et al. 2011) and a significant divergence in planktonic foraminiferal test size variance between low and high latitudes approaching the Eocene-Oligocene Boundary (Figure 5) (EOB, ~34 Ma) (Schmidt et al. 2004, 2006; Cramer et al. 2009, 2011; McGowran, 2012; Inglis et al. 2015).

The EOB marks the beginning of the “Icehouse” climate regime (Figure 5), and the most significant diversity loss (~35% extinction, Aze et al. 2011) amongst the macroperforate planktonic foraminifera since the K-Pg event (Figure 5). Extinction here appears to have been most severe amongst more ecologically and morphologically complex forms occupying the upper water column (Keller & MacLeod, 1992; Hallam & Wignall, 1997; Coxall & Pearson, 2007; Aze et al. 2011; Fraass et al. 2015; Lowery et al. 2020). This global transition was characterized by significant changes in water column structure, where the establishment of the Antarctic Circumpolar Current (ACC) and upwelling of cool, nutrient-rich bottom waters that accompanied the onset of permanent glaciation of the Antarctic mainland led to a dramatic deepening of the global Calcium Carbonate Compensation Depth (CCD) (Coxall et al. 2005; Schmidt et al. 2006; Edgar et al. 2007; Liu et al. 2009; Pälike et al. 2012; Villa et al. 2014; Sarkar et al. 2019; Wade et al. 2020; Dutkiewicz & Müller 2021; Hutchinson et al. 2021). Following the EOB extinction interval, macroperforate planktonic foraminifera exhibited a somewhat sustained period of "stasis" within their gross morphology and taxonomic richness which ensued for ~11 Myrs (Lowery et al. 2020) until the Oligocene-Miocene Boundary (Figure 5) (OMB, ~23 Ma).

The OMB was a global cooling event associated with further expansion of Antarctic icesheet volume (Beddow et al. 2016; Londoño et al. 2018; Steinthorsdottir et al. 2019; O'Brien et al. 2020), however, evidence suggests this cooling was terminated rapidly by warming of an approximately equal magnitude, and subsequent ice sheet retreat (Mawbey & Lear, 2013; Liebrand et al. 2017; Londoño et al. 2018; Steinthorsdottir et al. 2019). Following the initiation of the Neogene (~23 Ma), cryosphere intensification and macroperforate planktonic foraminiferal diversity continued to increase, despite the incidence of the Miocene Climatic Optimum (MCO, ~17-15 Ma), the youngest major high-CO_2 interval that interrupted the cooling trend which characterises the past 50 Myrs (Figure 5) (Holbourn et al. 2015). The period following the MCO is typified once again by Antarctic icesheet expansion (Shevenell et al. 2004; Holbourn et al. 2007; Frigola et al. 2018) which appears to have triggered increased efficiency of the marine biological carbon pump, allowing macroperforate planktonic foraminiferal evolutionary exploitation of new deep-water niches (Olsson, 1982; Scott, 1982; Keller, 1985; Malmgren & Berggren, 1987; Scott et al. 1990; Norris et al. 1993, 1994; 1996; Aze et al. 2011; Ezard et al. 2011; Boscolo-Galazzo et al. 2021). As global deep-sea temperatures continued to decline and surface habitats continued to change, increasing species richness culminated across the Miocene-Pliocene Transition (~7-4 Ma), exhibiting diversity levels comparable with the Eocene maximum (Figure 5) (Aze et al. 2011; Lamyman et al. in prep.). The significantly steeper latitudinal and water column temperature gradients of the Icehouse Ocean, coupled with the gradual closure of the Tethyan and Central American

Seaways (Crame & Rosen, 2002; Brierly & Fedorov, 2010; Hamon et al. 2013; Matthews et al. 2016; O'Dea et al. 2016), may have promoted greater endemism within Neogene macroperforate planktonic foraminiferal faunas (Scott et al. 1990; Rögl 1999; Norris, 1999, 2000; Kucera & Schönfeld, 2007; Crundwell, 2018; Rosenthal et al. 2018; Spezzaferri et al. 2018a; Lam & Leckie, 2020a; Kiss et al. in review) contributing to the observed rise in diversity (Aze et al. 2011; Ezard et al. 2011; Fraass et al. 2015; Lowery et al. 2020).

From ~3 Ma, species richness shows a notable decline approaching the Recent, despite the formation of permanent longitudinal and semi-permanent latitudinal dispersion barriers through continental reconfiguration and the Intensification of Northern Hemisphere Glaciation (Figure 5) (INHG) (Kleiven et al. 2002; Schmidt et al. 2004a; Cramer et al. 2009, 2011; Brierley & Fedorov, 2010; Willeit et al. 2015; Hayashi et al. 2020; Woodhouse et al. 2021). This loss of diversity approaching the Recent (Figure 5) is somewhat enigmatic, as greater limitations on pelagic dispersion would facilitate increased occurrences of geographic isolation suitable to certain modes of speciation (Mayr, 1942; Norris, 1999; 2000; Norris & Hull, 2012).

1.1.4 Speciation and extinction dynamics

The drivers of biodiversity in the oceans are fundamentally different to those observed for the terrestrial realm, largely due to the differences in the availability of sunlight and rates of temperature transfer between the two domains (Gagné et al. 2020). Dispersion mechanisms amongst pelagic marine microorganisms such as the planktonic foraminifera are particularly complex, being somewhat contemporaneous with fluid dispersion driven by wind, fluvial, or coastal currents (Ekman, 1953; Lazarus 1983; Norris, 1999; 2000; Sexton & Norris, 2008; Cowen & Sponaugle, 2009; Morrissey & de Kerckhove, 2009; Pringle et al. 2011; Norris & Hull, 2012; Norton, 2013; de Vargas et al. 2015; Steele et al. 2019; Faria et al. 2021). A comparative lack of physical dispersion barriers within the world's oceans would therefore appear to place limitations on the occurrence of extended periods of reproductive isolation necessary to certain mechanisms of speciation (Mayr, 1942; Norris, 1999; 2000; Norris & Hull, 2012). Though sympatric speciation is recorded within marine plankton (Lazarus et al. 1995; Pearson et al. 1997; Spencer-Cervato & Thierstein, 1997; Johannesson, 2009; Norris & Hull, 2012; Knappertbusch, 2016; Faria et al. 2021), there are examples within the planktonic foraminiferal record of speciation mechanisms facilitated by robust semi-permanent physical barriers (Lazarus, 1983; Motoyama, 1997; Wei & Kennett, 1988; Schneider & Kennett, 1999; Pearson & Ezard, 2014; Hull & Norris, 2009; Bicknell et al. 2018; Bendif et al. 2019; Woodhouse et al. 2021). Recent studies also highlight the scale of cryptic speciation present in the modern ocean, where globally distributed morphospecies are in fact made up of a suite of subtly morphologically distinct biological species with partial vertical and lateral habitat overlap (Darling & Wade, 2008; Aurahs et al. 2009; Morard et al. 2009, 2013; Ujiié et al. 2010; Weiner et al. 2012; 2014). Estimations of extant and fossil diversity can be further complicated however, by the morphological and taxonomic over-splitting of discrete genetic species which exhibit high polymorphism (André et al. 2013).

Several efforts in recent years have sought to examine and utilise the unparalleled resolution of the planktonic foraminifera fossil record to identify potential ecological and biogeographic pre-extinction signals which may better quantify organisms and ecosystems more susceptible to extinction risk. A wide spectrum of potential responses have been recorded through geochemical and morphological analyses of the group, most notably being the documentation of photosymbiont (Figure 3) “bleaching” during intervals of climate change (Figure 7) (Wade, 2004; Wade et al. 2008; Edgar et al. 2013a; Luciani et al. 2017; Si & Aubry, 2018; Shaw et al. 2021; Woodhouse et al. 2021). In the modern oceans photosymbiont bleaching amongst corals (Hughes et al. 2018) and larger benthic foraminifera (Schmidt et al. 2011; Spezzaferri et al. 2018b) is commonly driven by heat stress. Experimental results on living planktonic foraminifera (Bé et al. 1982; Caron et al. 1982), and multiple geochemical studies on fossil populations appear to confirm this phenotypic response to thermal drivers is replicated in extinct planktonic foraminifera during the hyperthermals of the early Cenozoic (Figure 5) (Wade, 2004; Wade et al. 2008; Edgar et al. 2013a; Si & Aubry, 2018; Shaw et al.

2021). Recent studies, however, suggest bleaching may not be isolated to geological intervals associated with heightened temperatures and may be a common pre-extinction response when taxa are subjected to a whole suite of selection pressures (Woodhouse et al. 2021).

Increased polymorphism and morphological character change often accompany changing shell geochemistry in the lead up to planktonic foraminiferal extinction (Wade et al. 2008; Edgar et al. 2013a; Woodhouse et al. 2021). Changes in morphology are of particular interest to conservation science as larger taxa within phylogenies are more susceptible to environmental selection pressures due to their heightened resource requirements and slower rates of reproduction (Riveros, 2007). In particular, large-scale extinction events are commonly manifested by the loss of larger, often structurally specialized species and diminished size amongst survivor taxa (Norris, 1991; Witting, 1997; Twitchett, 2007; Wade & Twitchett, 2009). Both of these responses are observed across the K-Pg and EOB extinction events within the planktonic foraminifera (Wade & Olsson, 2009; Pearson & Wade, 2015; Lowery & Fraass, 2019).

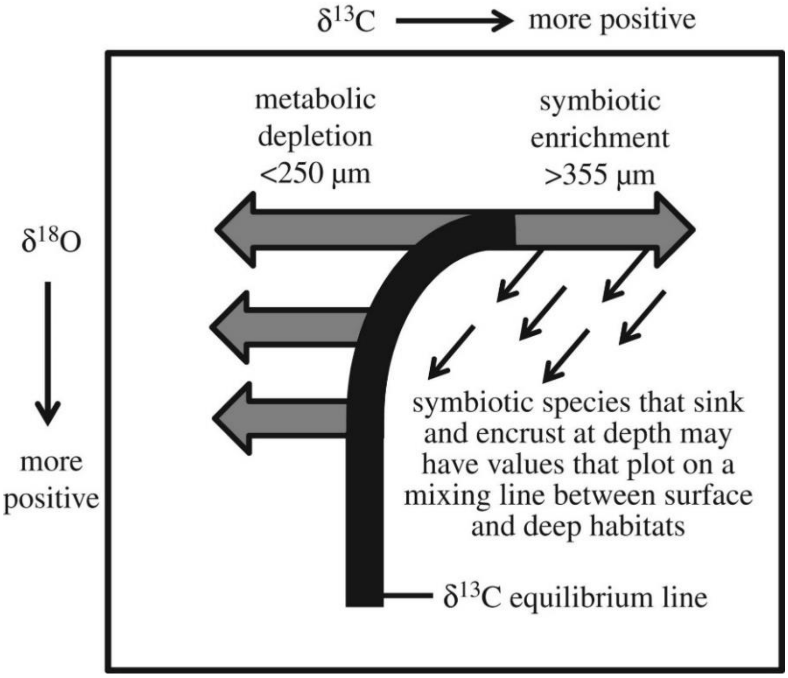

Figure 7. Schematic of $\delta^{18}O$ and $\delta^{13}C$ values of planktonic foraminifera which can be used to determine the depth habits and symbiotic relationships of modern and fossil species. From John et al. (2013).

A strong positive correlation exists between test size and the magnitude of global marine latitudinal and vertical temperature gradients in the Cenozoic planktonic foraminiferal fossil record, and despite the observation that larger test size does not necessarily dictate ecological optima (Schmalhausen, 1949; Rillo et al. 2018), greater size and absolute abundance are generally indicative of species-specific environmental suitability (Hecht, 1976; Schmidt et al. 2006). A general trend towards dwarfing is observed in modern planktonic foraminifera when subjected to unstable eutrophic conditions (Phleger, 1960; Wade & Olsson, 2009), and pre-extinction dwarfing is well-documented within the planktonic foraminiferal fossil record (Wade & Olsson, 2009; Wade & Twitchett, 2009; Brombacher et al. 2017; Falzoni et al. 2018; Brombacher et al. 2021). However, a whole suite of morphological alterations can be observed in response to selection pressures, including changes in calcification, growth asymmetry and even pre-extinction gigantism (Knappertbusch, 2007; Weinkauf et al. 2014, 2019; Fox et al. 2020; Todd et al. 2020; Woodhouse et al. 2021). Species may act to improve their mean population fitness via rapid character change, producing offspring with higher inter-individual phenotypic variability during periods of detrimental environmental change (Slatkin, 1974; Bull, 1987; Phillipi & Seger, 1989; Harvey & Pagel, 1991; Williams, 1992; Grafen, 1999; West-Eberhard, 2003). Pre-extinction dwarfing may in fact be a morphologically stable end result of such rapid character changes, producing populations typified by neotenic descendant populations with higher fecundity that are able to outlast their larger ancestors (Norris, pers. comm.).

Studies on the nature of species biogeography report the spatial expansion and contraction of taxa through their stratigraphic ranges (Foote, 2003, 2007, 2014, 2016; Jernvall & Fortelius, 2004; Foote et al. 2007, 2008, 2016; Liow & Stenseth, 2007; Liow et al. 2010; Tietje & Kiessling, 2013; Žliobaitė et al. 2017; Hohmann & Jarochowska, 2019), where ultimately, a trajectory of contraction in geographic range size leads to heightened extinction risk (Vrba, 1985; Jenkins, 1992b; Purvis et al. 2000; Finnegan et al. 2015; Hull et al. 2015; Urban, 2015; Saupe et al. 2015; Stanton et al. 2015; Kiessling & Kocsis, 2016; Smits & Finnegan, 2019; Brombacher et al. 2021). Though planktonic foraminifera demonstrate this general pattern (Liow et al. 2010), high-resolution analyses document spatial heterogeneity of populations in response to environmental pressures (e.g., Jenkins, 1992a; Scott et al. 2007;

Jonkers et al. 2019; Antell et al. 2021; Brombacher et al. 2021; Sexton pers. comm.), revealing characteristics of both the demographic (contraction towards the population core) and contagion hypotheses (receding from unfavourable conditions) described by Channell & Lomolino, (2000).

1.1.5 Occurrence datasets

The wealth of scientific knowledge achieved through the study of the planktonic foraminiferal fossil record has encouraged efforts to catalogue and compile planktonic foraminiferal taxonomic (Jenkins, 1971; Postuma, 1971; Berggren, 1977; Blow, 1979; Kennett & Srinivasan, 1983; Bolli et al. 1989; Hemleben et al. 1989; Pearson, 1993; Spezzaferri, 1994; Olsson et al. 1999; Pearson et al. 2006; Aze et al. 2011; Huber et al. 2016; Schiebel & Hemleben, 2017; Wade et al. 2018; Young et al. 2019; Lamyman et al. in prep.) and occurrence data (Lazarus, 1994; Spencer-Cervato 1999; Diepenbroek et al. 2002; Lloyd et al. 2012a; Fenton et al. 2016b; Siccha & Kučera, 2017; Renaudie et al. 2020; Fenton & Woodhouse et al. 2021), which has led to the use of “big data” analyses targeted across a wide range of scientific disciplines (Aze et al. 2011; Ezard et al. 2011; Lloyd et al. 2012a; Fenton et al. 2016b; Cantalapiedra et al. 2019; Smits & Finnegan, 2019; Antell et al. 2021). The most recent effort to collate fossil occurrence data, Triton (Fenton & Woodhouse et al. 2021), compiles all previous Cenozoic planktonic foraminiferal occurrence datasets with the addition of newly generated deep time records. Triton now represents the largest group-specific fossil occurrence dataset ever created with 512,922 individual specimen occurrences, permitting the investigation of biogeographic patterns within the planktonic foraminifera record at a greater resolution than ever before.

1.2 Aims

In this thesis, I analyse the Cenozoic planktonic foraminiferal fossil record across multiple spatiotemporal scales to assess the evolutionary patterns of speciation and extinction across the group. The results generated through these multidisciplinary analyses have clear implications for expanding our understanding of the nature and mechanisms of evolution and extinction within the marine realm, and the extensive range of reported pre-extinction signals potentially represent features amongst the Cenozoic planktonic foraminifera that may act as sentinels of marine ecosystem function and pelagic extinction risk in the modern oceans.

Aim 1 – To produce a unified database of all planktonic foraminifera fossil occurrence data by compiling existing Cenozoic planktonic foraminiferal occurrence datasets with the addition of newly generated deep time records.

Chapter 1 presents the Triton database (Fenton and Woodhouse et al. 2021), which now represents the largest group-specific fossil occurrence dataset ever created with 512,922 individual specimen occurrences, permitting the investigation of biogeographic patterns within the planktonic foraminifera record at a greater resolution than ever before. This chapter is published as a joint first author contribution in Scientific Data: Fenton, I, Woodhouse, A., Aze, T., Lazarus, D., Renaudie, J., Dunhill, A., Young, J., and Saupe, E.E., 2021. Triton, a new species-level database of Cenozoic planktonic foraminiferal occurrences. Scientific Data, 8, 160. https://doi.org/10.1038/s41597-021-00942-7

Aim 2 – To investigate species geographic ranges in the lead up to their extinction and whether range decline trajectories are influenced by species ecology, overarching climate regime or rapid climate perturbations.

Chapter 2 presents statistical analysis of Triton occurrence data of the biogeographic range trajectories of species in the final third of their stratigraphic ranges. The analyses show a near consistent decline in species geographic range approaching extinction, although species ecologies can influence the rate of biogeographic decline prior to extinction, potentially through more flexible ecological niche adaptivity.

Aim 3 – To investigate the abiotic controls on the speciation locations and subsequent biogeographic ranges of Cenozoic planktonic foraminifera.

Chapter 3 presents statistical analysis of the occurrence data in the Triton database of speciation locations and subsequent species biogeographic ranges throughout the Cenozoic. Speciation in the Greenhouse regime of the early Cenozoic is dominated by extratropical speciation cradles, which are gradually complimented by the development of a tropical cradle during the descent into the Icehouse in the second half of the Cenozoic. Additionally, species which evolved in latitudes and water column depths, which are inherently subjected to stronger and more frequent environmental change, exhibit greater distances of population migration throughout their life histories.

Aim 4 – To investigate potential biological and ecological indicators of impending extinction through high-resolution morphometric and geochemical analysis of two* Dentoglobigerina *species that underwent extinction 3 million years ago.

Chapter 4 presents data generated from direct sampling of the fossil record of thousands of individual specimens using high-resolution, paired geochemical and morphological examination across the extinction interval of two evolutionary lineages of the genus *Dentoglobigerina* (Woodhouse et al. 2021). Analyses revealed a stepwise change in phenotypic characters of *Dentoglobigerina altispira* prior to extinction, where greater polymorphism precedes permanent ecological niche migration to a deeper depth habit. Whereas the contemporaneous closely related species *Dentoglobigerina baroemoenensis* exhibits “pre-extinction gigantism” and photosymbiont bleaching preceding its isochronous extinction. This chapter is published in Scientific Reports: Woodhouse, A., Jackson, S.L., Jamieson, R.A., Newton, R.J., Sexton, P.F., and Aze, T., 2021. Adaptive ecological niche migration does not negate extinction susceptibility. Scientific Reports, 11, 15411, https://doi.org/10.1038/s41598-021-94140-5

1.3 Account of the project

This project is funded by the NERC Studentship grant NE/L002574/1. The original project proposal aimed to produce high-resolution analysis of a number of planktonic foraminiferal extinctions across the last ~23 million years (Myrs) to determine whether extinction risk is linked to biogeographic range, species ecology, or morphological traits. After examination and discussion of the fossil record, it was clear that the majority of fossil occurrence data were absent from the available microfossil datasets, and a new database needed to be created. Moreover, due to the non-uniform biogeographic nature of extinction, it was decided that the investigation of morphological and ecological traits would focus upon the well-dated extinction of species from a single genus, the *Dentoglobigerina*.

The first year of the PhD project involved an assessment of the most up to date Cenozoic planktonic foraminiferal occurrence databases, and the identification of potentially well-represented extinctions. This year involved my participation in a number of training programs to become more proficient in the R programming language and improve my knowledge of Cenozoic planktonic foraminiferal taxonomy and scientific ocean drilling. These workshops included: the NERC Software Carpentry NOVICE Workshop in Bristol, UK; Taxonomy and Biostratigraphy of Cenozoic Planktonic Foraminifera at the Natural History Museum, UK; The ECORD Virtual Drillship Experience in Bremen, Germany; the R4All - Getting started with R workshop in Lancaster, UK, and both the Urbino International School on Foraminifera and Urbino Summer School on Paleoclimatology held in Urbino, Italy. I also submitted an application to sail onboard IODP Expedition 372B/375 to provide me with unique first-hand experience of the processes involved within scientific ocean drilling that would be beneficial to all aspects of this project. This application was ultimately successful, permitting me to sail the following academic year.

During the second year of the project, following the inspection of the extinction intervals across a number of species, I decided to focus morphological and ecological analysis on a single genus, *Dentoglobigerina,* which documented high abundances, and large adult test sizes suitable for single specimen stable isotope analysis up until their extinction horizon. Well-dated samples were ordered from the IODP repository and processed prior to leaving for IODP Expedition 372B/375, which required me to take an 8-month hiatus from my studies to sail and conduct post-cruise research. During the Spring of the second year, I successfully applied to the University of Leeds Laidlaw Scholarship Programme to employ an undergraduate student to begin morphometric work on *Dentoglobigerina* specimens whilst I also worked on my post-cruise objectives. This work ultimately became the student's undergraduate dissertation topic and contributed towards the morphological data of Woodhouse et al. (2021). Additionally, after ongoing discussion with Dr Isabel Fenton, and Dr Erin Saupe of the University of Oxford, the decision was made to collaborate on the creation of a new Cenozoic planktonic foraminiferal occurrence dataset.

The third year of the project was mainly focussed on primary data acquisition for the analysis of the extinction of *Dentoglobigerina* (Woodhouse et al. 2021). All individual specimens had to be imaged from multiple angles, and morphometric data extracted and processed. Specimens had to also be individually cleaned and analysed for stable isotope ratios to determine their ecology.

The fourth year involved continuation of the interpretations of *Dentoglobigerina* data and creation of the manuscript detailing the extinction (Woodhouse et al. 2021). We also agreed upon the objectives and allocation of labour for the creation of the new Cenozoic planktonic foraminiferal dataset. I reviewed and collated all ocean drilling records that were missing from previous efforts, assessed the stratigraphic completeness of ocean cores, then extracted all site-specific chronostratigraphic data for the creation of discrete age models (Fenton & Woodhouse et al. 2021). It was during this year I also had the misfortune of becoming stranded in New Zealand for three months due to the COVID-19 pandemic while on my way to attend the IODP Expedition 372/375 postcruise-meeting, however I was able to continue working on manuscripts and databases remotely, although under much more challenging circumstances than had I been in the U.K. with my desktop computer.

The fifth and final year saw the completion, submission, and acceptance of the study on morphological and ecological pre-extinction dynamics of *Dentoglobigerina* (Woodhouse et al. 2021), as well as the publication of Triton, our collaborative Cenozoic planktonic foraminifera occurrence dataset (Fenton & Woodhouse et al. 2021). Once Triton was finalised for publication in the Spring, I was able to perform statistical analyses on the biogeographic dynamics of speciation and extinction within the Cenozoic macroperforate planktonic foraminifera, the results of which are now being written up for publication.

1.3.1 Co-supervised undergraduate research projects

During my time at the University of Leeds, my supervisor Dr Tracy Aze actively encouraged me to formulate research topics of benefit to students on Leeds undergraduate programs that would link to my research interests. In total, I co-supervised three novel research projects exploring planktonic foraminiferal ecology.

Project Title: "Extinction dynamics of Dentoglobigerina altispira"

Sophie Jackson – BSc Environmental Science

Background and Rationale: During the summer of 2018/19, I was successful in my application to the University of Leeds Laidlaw Scholarship Programme to allow an undergraduate to assist with a research project. The student generated primary data on the extinction of the planktonic foraminiferal species *Dentoglobigerina altispira* (Figure 2), which formed the basis of the morphometric data detailed in Woodhouse et al. (2021).

Project Title: "Deciphering the palaeoceanographic signatures of Planktonic Foraminifera to determine the tectonic migration of the Hikurangi Plateau"

Megan Murphy – BSc Environmental Science

Background and Rationale: Coring at IODP Expedition 372B/375 Site 1526B recovered ~30 m of hiatus-bounded pelagic sediments on Tūranganui Knoll which yielded well-preserved planktonic foraminifera of Holocene-Maastrichtian age (Wallace et al. 2019). After exceptional preservation of planktonic foraminifera was discovered through three temporal intervals with the core (Pleistocene, Pliocene, Maastrichtian) I formulated a research project that would utilise the ecological groupings (Aze et al. 2011), and stable isotopic geochemistry of assemblages to reconstruct the paleoceanographic conditions of the three discrete time periods.

Project Title: “The biogeographical modality range response of Planktonic Foraminifera to Cenozoic climate upheavals to elucidate how future climate change might influence global biodiversity” Jake Herman – BSc Environmental Science

Background and Rationale: Following the construction of the Triton dataset (Fenton & Woodhouse et al. 2021), I created a research project which would utilise the greatly enhanced sampling resolution of the Cenozoic planktonic foraminiferal record to assess spatial changes within species across major climatic events.

1.3.2 International Ocean Discovery Program Expedition 372B/375: March-May 2018

During the second year of my PhD studies, I sailed onboard IODP Expedition 372B/375, operating as a shipboard foraminiferal biostratigrapher. The primary aim of the expedition was to analyse the occurrence of slow slip events (SSEs) across the Hikurangi Subduction Margin. SSEs are tectonic events involving transient aseismic slip across a fault which occur over weeks to years at velocities intermediate between plate tectonics and slip velocities which generated seismic waves (Saffer et al. 2019). The northern Hikurangi subduction margin hosts some of the best-documented, and shallowest occurring SSEs on Earth (Wallace & Beavan, 2010; Wallace et al. 2016), allowing for quantification of the geological properties and the direct monitoring of SSEs through scientific drilling and the installation of subseafloor observatories.

The primary aims for IODP Expedition 372B/375 were:

1. Characterize the incoming sedimentary sequence on the incoming subducting Pacific plate along the Hikurangi subduction margin.
2. Characterize material and physical properties of sediments above the SSE region.
3. Install subseafloor observatories in the Pāpaku fault along the deformation front within the overriding plate to provide direct monitoring of subseafloor physical properties associated with SSEs.

Operations during IODP Site 375-1520 recovered a depositional system dominated by terrigenous gravity flow processes to a pelagic carbonate system of Holocene to early Paleocene age (Barnes et al. 2019). Below this, a volcaniclastic gravity flow system dominated the sedimentary record down to the occurrence of alternating volcaniclastic conglomerates and clayey siltstones and siliceous mudstones of Late Cretaceous age (Barnes et al. 2019). My post-cruise objectives from Expedition 372B/375 include the characterisation of late Pleistocene sedimentary systems, and biostratigraphic and palaeoceanographic investigations of pre-Neogene sediments. Furthermore, I am an associate investigator on the Marsden Grant funded project: “Does climate influence the frequency of volcanic activity and earthquakes?”. This project involves an international team of biostratigraphers and sedimentologists utilising the extraordinarily high sedimentation rates of New Zealand’s active margin to test the regional link between late Pleistocene glacial-interglacial cycles on the frequency of volcanic eruptions and earthquakes.

1.3.3 Postcruise research outputs

Crundwell, M.P., and Woodhouse, A., Biostratigraphically constrained chronologies for Quaternary rocks from IODP Expeditions 372 and 375, Hikurangi margin (East Coast Basin), New Zealand, *Submitted*.

Contributions: This manuscript includes the shipboard biostratigraphy which I helped generate on IODP Expedition 372B/375.

Noda, A., Greve, A., Woodhouse, A., and Crundwell, M.P., Depositional rate, grain size and magnetic mineral sulfidization in turbidite sequences, Hikurangi Margin, New Zealand, *Submitted.*

Contributions: This manuscript includes a benthic foraminiferal oxygen isotope age model, created with data I generated at the University of Leeds from IODP Site 1520D.

Woodhouse, A., Barnes, P., Shorrock, A., Strachan, L.J., Crundwell, M.P., Hopkins, J., Bostock, H.C., Kutterolf, S., Pank, K., Greve, A., Cook, A., Petronotis, K., Levay, L., Underwood, M., Bell, R., Jamieson, R.A., Aze, T., Wallace, L., Saffer, D., Pecher, I., Sedimentation response to glacio-eustatic sea-level cyclicity over the last 40 ka, Hikurangi subduction margin, New Zealand, *In. prep.*

Contributions: As lead author, I have compiled a number of datasets, and have generated planktonic and benthic foraminiferal oxygen isotope records at the University of Leeds from IODP Site 1520D. This data assists AMS-^{14}C and volcanic tephra dates to reconstruct sedimentation response of the Hikurangi subduction margin to late Pleistocene sea level fluctuations. In additional planktonic and benthic foraminiferal faunas are used to assess reworking and *in situ* faunas.

Woodhouse, A., Malié, P., Shepherd, C., Crundwell, M.P., Williams, O., Hollis, C., Wallace, L., Saffer, D., Pecher, I., Barnes, P., Aze, T., Mid-Cretaceous organic-rich sedimentation on the Hikurangi Plateau, *In prep.*

Contributions: As lead author, I have analysed the planktonic and benthic foraminiferal assemblages to assess the age and palaeoceanography of the mid-Cretaceous strata from IODP Site 1520C. I have also performed stable isotope analysis of selected well-preserved planktonic and benthic foraminifera at the University of Leeds.

2. Triton, a new species-level database of Cenozoic planktonic foraminiferal occurrences

Authors

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Abstract

Planktonic foraminifera are a major constituent of ocean floor sediments, and thus have one of the most complete fossil records of any organism. Expeditions to sample these sediments have produced large amounts of spatiotemporal occurrence records throughout the Cenozoic, but no single source exists to house these data. We have therefore created a comprehensive dataset that integrates numerous sources for spatiotemporal records of planktonic foraminifera. This new dataset, Triton, contains >500,000 records and is four times larger than the previous largest database, Neptune. To ensure comparability among data

sources, we have cleaned all records using a unified set of taxonomic concepts and have converted age data to the GTS 2020 timescale. Where ages were not absolute (e.g., based on biostratigraphic or magnetostratigraphic zones), we have used generalised additive models to produce continuous estimates. This dataset is an excellent resource for macroecological and macroevolutionary studies, particularly for investigating how species responded to past climatic changes.

2.1 Background & Summary

Planktonic foraminifera are unicellular zooplankton found throughout the world's oceans. They have calcareous shells or ‘tests’ with morphological variation that allows for specimens to be identified to species level. The morphological species concepts used to identify foraminifera species based on test characteristics agree approximately with genetic species concepts[1-3], with the level of cryptic speciation seemingly no more frequent than in other groups e.g. Agapow, et al. [4]. On death, many of their calcareous tests are deposited on the ocean floor, where they contribute – often in significant amounts – to the sediment[5]. Consequently, planktonic foraminifera have one of the most complete species-level fossil records of any group[6].

The fossil record of planktonic foraminifera has been used to study fundamental evolutionary and ecological questions, such as the relative role of abiotic versus biotic drivers in clade diversification[7], the temporal persistence of large-scale ecological patterns such as the latitudinal biodiversity gradient[8], the importance of fossils for understanding diversity dynamics[9], and the potential of ancient extinction events to inform conservation today[10]. Our new database of planktonic foraminifera occurrence data aims to broaden the potential and increase the accuracy of analyses that address these and other key ecological and evolutionary questions.

Over the past 50 years, a series of international projects have sampled seafloor and sub-seafloor sediments, including the Deep Sea Drilling Project (1968-1983), the Ocean

Drilling Program (1985-2004), the Integrated Ocean Drilling Program (2004-2013) and the International Ocean Discovery Program (2013-2023). Of 375 expeditions, 158 have published species-level data on planktonic foraminifera, whether for biostratigraphic purposes or community analyses as part of results from cruise activity (e.g. Saffer, et al. [11],Tamura, et al. [12]) or later reanalyses of the data, producing a wealth of palaeobiological data[13]. Many smaller, primarily piston or drop-core expeditions have also produced useful species-level data on planktonic foraminifera. However, no single, easily accessible resource exists that documents spatiotemporal records from these sources. Previous databases of planktonic foraminifera either contain only a subset of existing samples (e.g. Neptune[14-16]), or hold data in an archive structure, consisting of many separate datasets in different formats e.g. PANGAEA[17].

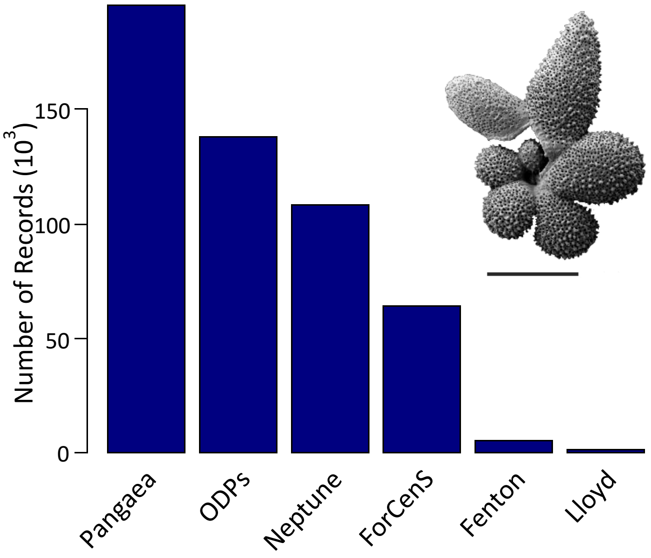

Figure 1. The number of records (in 1000s) from each of the different data sources in Triton. The referenced data sources are: Pangaea[17], ODPs (ocean drilling projects: DSDP, ODP and IODP), Neptune[14-16], ForCenS[21], Fenton, et al. [8], Lloyd, et al. [22]. Inset: *Globigerinella adamsi*, an example planktonic foraminiferal specimen from the Paleogene GLObal Warming events "GLOW" cruise[44], Southwest Indian Ocean, scale bar = 200 µm.

Here we describe the creation of Triton, a species-level occurrence-based dataset that brings together planktonic foraminiferal sediment data for the Cenozoic from multiple sources (Fig. 1). The data are curated to ensure consistency in metadata across different sources. The taxonomy is updated to ensure consistency with publications of the Paleogene and Neogene

Planktonic Foraminifera Working Groups (see “PFdata” in the figshare data repository[18]). Age models are similarly updated to the GTS 2020 timescale[19], and, where necessary, more precise age models are calculated. Paleo-coordinates of fossil samples are estimated using a single plate rotation model. The new methods developed for Triton and described in this paper can be applied across sediment samples for other fossil groups.

Triton provides a single access point for comprehensive spatio-temporal planktonic foraminifera data across the Cenozoic. It contains four times as many records as the previous largest planktonic foraminiferal distribution database, Neptune, and has a more comprehensive latitudinal spread through time (Table 1, Fig. 2). Diversity curves through time plotted from the Triton data indicate major features of species richness changes in planktonic foraminifera (Fig. 3), such as the end Eocene extinctions at 34 Ma[7,20]. These raw diversity curves depict a number of macroevolutionary events that were only apparent in Neptune once subsampling methodologies were applied, suggesting Triton has significantly more complete sampling. The Triton database offers many new opportunities for the use of planktonic foraminifera for a broad range of global studies or regional studies. These could be of a biological focus, based on ecological, evolutionary or conservation questions, for example investigating the past responses of planktonic foraminifera to drivers such as climate over a range of timescales. Alternatively, they could be geochemical questions, such as which cores contain abundant records of particular species for isotopic analyses, or oceanographic studies, investigating changes in ocean circulation or upwelling through time as a result of climatic or tectonic changes.

2.2 Methods

2.2.1 Data sources

No single comprehensive dataset of planktonic foraminiferal distributional records currently exists. Instead, these data are available from a wide range of sources in many different structures. Some of these sources are compilations of existing data (e.g., Neptune[14-

[16], ForCenS[21]), and others derive from individual sampling sites (e.g. ocean drilling expeditions). Triton combines these disparate sources (Fig. 1) to produce a single spatio-temporal dataset of Cenozoic planktonic foraminifera with updated and consistent taxonomy, age models, and paleo-coordinates.

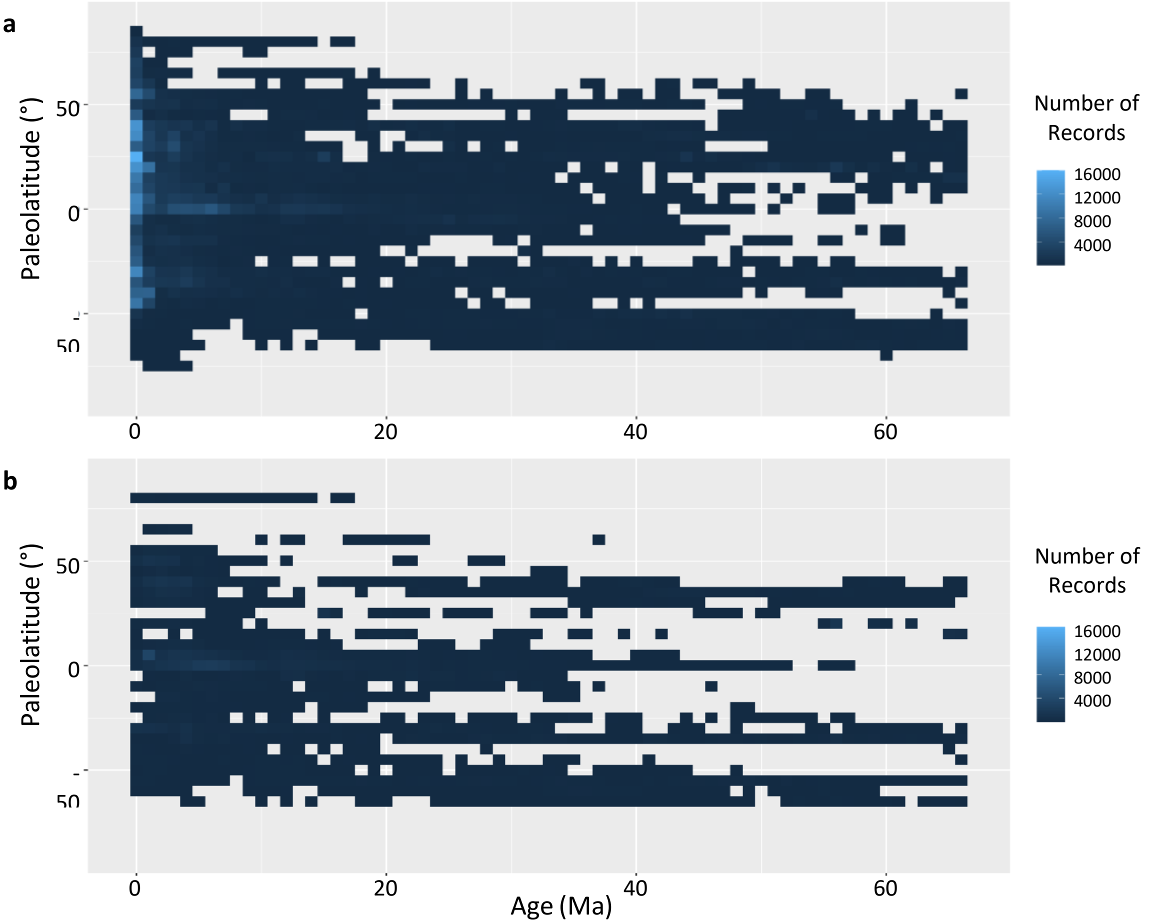

Figure 2. The latitudinal spread of data through time, showing (a) Triton and (b) the current data in Neptune. The squares are coloured to show the number of records, where a record is a row in the database (i.e., a species at a given location for a given age).

Neptune is currently the most comprehensive database of fossil plankton data, with records exclusively from the DSDP, ODP and IODP representing planktonic foraminifera, calcareous nannofossils, diatoms, radiolaria and dinoflagellates[14-16]. A subset of these sites is included in Neptune, representing those with the most continuous sampling through time. The raw data from Neptune form the core of our dataset. All foraminiferal occurrences for the Cenozoic (i.e., last 66 Ma) were downloaded using the GTS 2012 timescale. In the download options, all questionable identifications and invalid taxa were removed, as were records that had been identified as reworked.

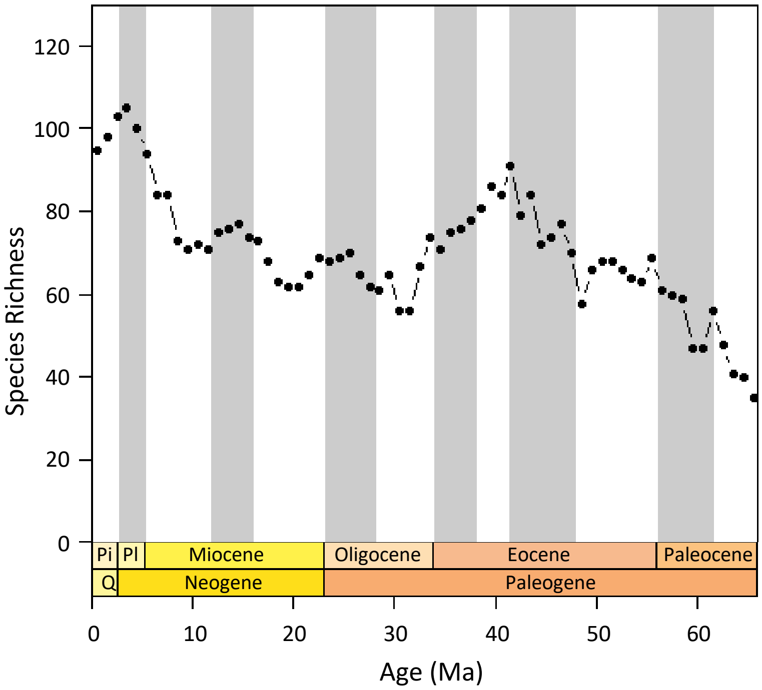

Figure 3. Species richness through time estimated from Triton (i.e., the number of species in each 1 Ma time bin). The pattern observed in Triton matches our understanding of diversity through the Cenozoic, particularly capturing the extinctions that occur at the end of the Eocene at 34 Ma[7]. The vertical lines indicate geological stages. Pl – Pliocene; Pi – Pleistocene. Note this plot uses the trimmed version of the data.

In addition to Neptune, three other compilation datasets were included in Triton: ForCenS[21], which consists of global core-top samples; the Eocene data from Fenton, et al. [8] created based on literature searches for planktonic foraminiferal data in the Eocene; and the land-based records from Lloyd, et al. [22] that were created from literature searches. The marine records in Lloyd, et al. [22] were not included, as they were obtained from Neptune.

Following preliminary compilation of existing datasets, we identified all legacy DSDP, ODP and IODP cores missing from Triton. The online DESCLogik (http://web.iodp.tamu.edu/DESCReport/) and Pangaea[17] databases were then mined for .csv files containing planktonic foraminiferal species count data for the missing cores, supplemented with data from AWI_Paleo (URI:

http://www.awi.de/en/science/geosciences/marine-geology.html), GIK/IFG (URI: http://www.ifg.uni-kiel.de/), MARUM (URI: https://www.marum.de/index.html), and QUEEN (URI: http://ipt.vliz.be/eurobis/resource?r=pangaea_2747#contacts). All additional cores were assessed individually by inspecting the scientific drilling proceedings to determine whether sites were suitable to contribute to our dataset. The primary assessment criterion was identification of continuous sedimentary sections, wherein two or more confidently assigned consecutive chronostratigraphic tie points existed to allow for construction of age models.

In addition to these longer cores, many sediment sampling projects have produced planktonic foraminiferal distribution data from shorter cores that tend to correspond in age to the last few million years. The website PANGAEA[17] (www.pangaea.de) has been used as a repository for most of these occurrence data. This website was searched using the terms "plank* AND foram", with resulting datasets downloaded using the R package 'pangaear'[23]. These datasets were filtered to exclude records collected using multinets, sediment traps or box cores, as these methods produce samples not easily correlated to sediment cores. Column names allowed for further filtering to exclude records with no species-level data, records that had only isotopic data (rather than abundance data), or records with no age controls.

2.2.2 Data processing

The data sources underpinning Triton serve their records in different formats. Therefore, processing was necessary to convert records into a unified framework, with one species per row for each sample and associated metadata (see below for details). Some metadata could be used without modification when available (e.g., water depth, data source), whereas other data needed processing to ensure consistency (e.g., abundance, paleo-coordinates, age). Without this processing, samples from different sources were not directly comparable. Where data were not available, they were set to NA. Those records with missing data in crucial columns (species name, abundance, age, and paleo-coordinates) were removed from the final dataset. All data processing was performed using R v. 3.6.1[24].

Taxonomic consistency is essential to enable comparison of datasets created at different times. The species and synonymy lists used in Triton are based on the Paleogene Atlases[20,25,26], with additional information from mikrotax[27] (http://www.mikrotax.org/pforams/). These sources were supplemented, when necessary with more up to date literature including Poole and Wade [28] and Lam and Leckie [29]. (A full list of the taxonomic sources can be found in the PFdata.xlsx file[18].) A synonymy list was generated to convert species names to the senior synonym. At the same time, typographic errors were corrected. For example, *Globototalia flexuosa* should be *Globorotalia flexuosa*. Exclusively Mesozoic taxa were omitted, as were all instances when species names were unclear or imprecise (i.e., not at the species level). Junior synonyms were merged with their senior synonyms and their abundances summed, although the original names and abundances are also retained in the processed dataset. For presence/absence samples, these numerical merged abundances were set to one (i.e., present). The full species list and list of synonyms can be found in the accompanying data.

Abundance data for planktonic foraminifera are provided in different formats: presence/absence, binned abundance, relative abundance, species counts, and number of specimens per gram. These metrics were converted into numeric relative abundance to make comparisons easier, although both the original abundance value and its numeric version are retained, as is a record of the abundance type. Presence/absence data were converted to a binary format (one for present; zero for absent). Species counts were converted to relative percent abundances based on the total number of specimens in the sample (this was calculated where it was not already recorded). When full counts were not performed, binned abundances were frequently used. These binned abundances were converted into numeric abundances based on the sequence. So, for example, the categorical labels of N, P, R, F, C, A, D (indicating none, present, rare, few, common, abundant, dominant) were converted to a numerical sequence of 0 to 6. As the meaning of letters can depend on the context (e.g., ‘A’ could be absent or abundant), conversion was done in a semi-automated fashion on a sample-by-sample basis. A value of 0.01 was assigned to records where an inconsistent abundance was recorded (e.g., samples with mostly numeric counts but a few species were designated ‘P’, indicating presence). Samples with zero abundance were retained in the full dataset to provide an indication of sampling.

The age of samples were recorded in multiple ways. For some samples, age models provide precise numerical estimates of the age (e.g., those in Neptune). Other samples are dated relative to stratigraphic events such as biostratigraphic zones (including benthic and planktonic foraminifera, diatoms, radiolarians and nannofossils) or magnetic reversals. In this case, ages sometimes needed to be converted to reflect revised age estimates. The start and end dates of biostratigraphic zones are defined in relation to events in marker species, e.g., their speciation, extinction, or acme events. All such marker events were updated to their most recent estimates and tuned to the GTS 2020 timescale[19]. The process of updating included correction of synonymies. Additional care was taken to ensure the correct interpretation of abbreviations (e.g., determining whether LO meant lowest occurrence or last occurrence) based on the entire list of events for a study. Where up-to-date ages were not available or events were ambiguous, they were removed from the age models.

The marker events defining a zone can depend on the zonal scheme used. For example, Berggren[30] defined the base of the planktonic foraminifera zone M8 as the first occurrence of *Fohsella fohsi*. Wade et al[31] used this same event to define the base of M9. Therefore, the zonal scheme was recorded when collecting age models, to accurately convert ages to the GTS 2020 time scale. Some marker events have different ages depending on the ocean basin or latitude, and these differences are not necessarily well studied[31,32]. Where these differences in marker events have been recorded, the coordinates of a site were used to determine whether sites were in the Atlantic or Indo-Pacific Ocean, and whether they were tropical or temperate (with the division at 23.5° latitude). However, this is an area where more research is needed to improve the accuracy of higher-latitude dating[32]. Magnetostratigraphic ages were also tuned to the GTS 2020 timescale.

We constructed new age models for samples not already assigned a numeric age. Where the depths of biostratigraphic events were already recorded, these were converted directly to GTS 2020. Where samples were not given any ages, often the case for the cores collected in the early days of ocean drilling, ages were reconstructed from the shipboard and post-cruise biostratigraphic data available in DESCLogik, Pangaea, and drilling publications. For holes where no tie point data were retrievable, biostratigraphic count data were extracted directly from drilling publications, and biostratigraphic events were assigned via GTS 2020. The first and last occurrences in raw shipboard biostratigraphic data often do not represent true datums, and careful assessment of the shipboard, and post-cruise literature was a prerequisite to confidently assigning chronostratigraphic datums. Tie point depths were assigned as the midpoint depth between the core sample before and after an event. For example, for an extinction event, the recorded depth was the midway point between the last recorded occurrence of a species and the first sample from which the species is absent. All sites were assessed individually to determine the age of the seafloor. Where IODP reports or sample-based publications strictly stated that the sediment surface (i.e., 0.00 meters below seafloor (mbsf)) was deemed to be "Holocene", "Recent" or "Modern" in age, an additional 0 Ma tie point was assigned appropriately. All samples present outside the maximum/minimum age tie points for that site were removed, as they could not be confidently assigned an age. During assessment, individual drilling reports were investigated for geological structures. Where features such as unconformities, reverse faults, stratigraphic inversions, décollements, and major slips and slumps were identified, separate age models were generated for individual intact stratal intervals to account for potential externally emplaced or repeated strata (see "Age models" and "Triton working" in the figshare data repository[18]). Similarly, age gaps of greater than 10% of the age range of the core were classified as hiatuses, leading to separate age models (see Fig. 4). Cores of denser sediments that have been sampled using rotary drilling will often have only ~50-60% recovery in a core (9.5m)[33]. As it is not possible to determine where the recovered core material came from within this length, all intact core pieces are grouped together as a continuous section from the section top, regardless of where the pieces were sourced (e.g., 4.5 m of recovered material will be recorded as 0-4.5 m of cored interval even if some came from 9-9.5 m). Consequently, age estimates within cores where recovery was low, typically the samples collected longer ago, will necessarily be less certain.

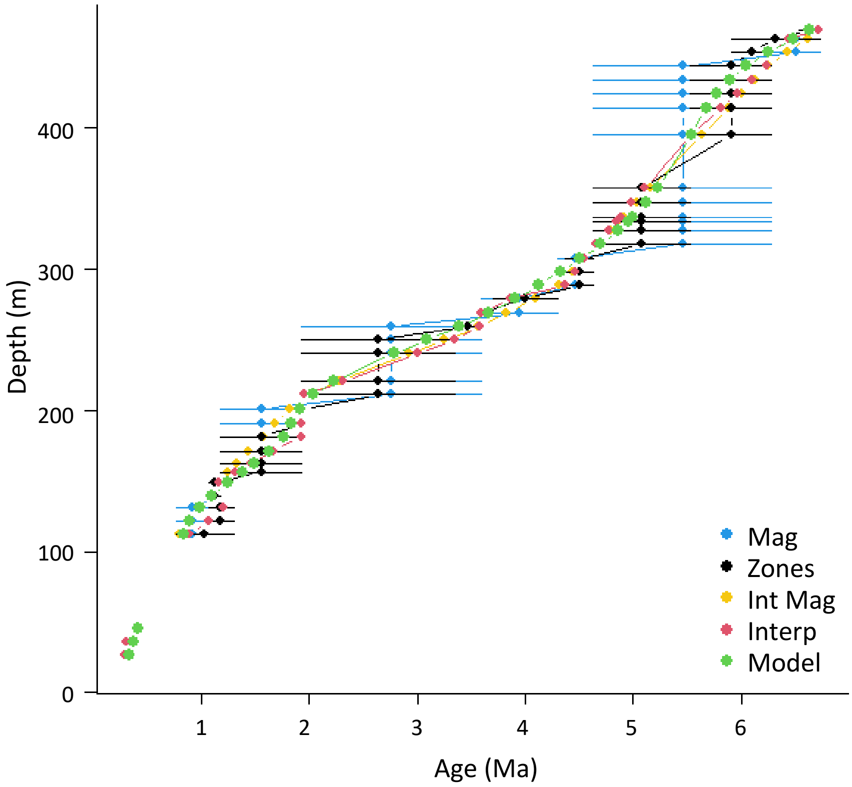

Figure 4. Different age model estimates applied to core material from IODP Site U1499A in the South China Sea. Mag – mean age based only on the magnetostratigraphic marker events. Zones – mean age based on all the marker events. Int Mag – interpolation of the points between the magnetostratigraphic marker events. Interp – interpolation between the full set of marker events. Model – the model of age as a function of depth. Note the hiatus between 50 and 100m. For the shallower section of the dataset, with only three data points, a simple linear model was used. For the deeper section, a GAM smooth was fitted. For this site, the model predictions were chosen as the best fit.

Using the updated marker event ages, we created age-depth plots and modelled the best fit to the data. There are different ways of creating these models, and multiple methods were applied to each core. The one that provided the best fit to the original data was chosen (the different age models are available in “Age models” in the figshare data repository[18]). These choices were confirmed manually (see Fig. 4). The simplest age model used interpolation of the marker events to create ‘zones’ and assign estimated ages assuming a continuous sedimentation rate between the start and end of each of these zones. Where the events do not provide a continuous sequence (e.g., gaps in the zonal markers), age estimates were assigned as the mean of that zone with error estimates of the width of the zone. Where magnetostratigraphic events were present, they were given preference. This method leads to different estimates of sedimentation rate for each zone. The more complex age model estimates a smoother sedimentation rate. When there were fewer than 5 marker events, a linear model of age as a function of depth was fitted for the entire core. For larger datasets, generalised additive models (GAMs) for the same variables were used, to allow for variation in sedimentation rates through time. GAMs were run using the mgcv R library, with a gamma value of 1.1[34]. The type of age model used in the analysis was recorded. Where appropriate, the number of points and the r^2 of the model are recorded to give an indication of the accuracy of the age model.

The latitude and longitude coordinates of samples were recorded in decimal degrees. For all samples except modern ones, plate tectonic reconstructions were necessary to determine the coordinates at which the sample was originally deposited. Reconstructions were performed using the Matthews, et al. [35] plate motion model, which is an updated version of the Seton, et al. [36] model used by Neptune. Comparisons of age models[35-39] suggest this model is most appropriate for the deep sea environment where most of the samples occur, and is able to assign coordinates to significantly more sites than the Scotese [39] GPlates model. This test was performed with a subset of the data (10633 unique sites); the Matthews, et al. [35] model provided paleocoordinates for 95% of the data, whilst the GPlates model only provided coordinates for 17% of the data. The calculation of paleocoordinates was automated using an adaptation of https://github.com/macroecology/mapast.

When sediment samples are derived from multiple sources, duplication will inevitably occur. All such duplicated records, identified based on the combination of species, abundance, sample depth, and coordinate values, were removed. Additionally, working on an individual record level, species that occurred significantly outside their known ranges were flagged (following updated age models) on the assumption these records were misidentifications, contamination, or re-working. Records were classified as falling significantly outside their known range if they were more than 5 Ma outside the species' range in the Palaeogene (66-23 Ma) and more than 2 Ma in the Neogene (23-0 Ma). These values were chosen based on the tradeoff between removing reworked specimens and allowing for some errors in the age estimates. Age estimates for older samples tend to be less precise. Ages were obtained from Lamyman et al (in prep) and are available in "PFdata" in the figshare data repository[18]. In total, 10,990 suspect records were flagged (~2 % of all records).

2.2.3 Data Records

The final dataset ("Triton" in the figshare data repository[18]) consists of one row per species for each sample depth from a core site. The associated metadata for these records can be categorised into a set of groups relating to the source of the data, the abundance of the species, the age of the sample, the geographic position of the site, the ocean drilling information (where appropriate), and the sampling procedures followed. These categories are explained in detail below.

The source of the data (**source**) is recorded based on the data citation and **year** in which it was collected. The primary data sources (e.g. Neptune, Pangaea) are given unique IDs (**db.source**). Individual datasets within this are given unique IDs (**db.ID**); these are particularly relevant for Pangaea where multiple, separate datasets exist. Each site is given a unique **holeID**, and samples within sites are designated using the **sampleID** (which is a unique number added to the **holeID**). The **rowID** is created by combining the database ID, the **sampleID**, and a unique number assigned to each row (i.e., species). The **person** who entered the data and **date** of the most recent update of that entry is also recorded.

The original species names assigned are listed in (**orig.species**). Where species were identified as synonyms and their records merged, both names are included in this column separated by a comma. The **species** column records the currently accepted name. Similarly, the original abundance column (**orig.abundance**) contains the abundance (or abundances for synonyms separated by commas) in its original form. The abundance units (**abun.units**:

relative abundance, count, number per gram, binned, presence/absence) are recorded. **Abundance** is a numeric version of the abundance (**orig.abundance**). Where the number of counted individuals was recorded, it is provided in the **total.IDd** column. This total is also included in the number of individuals (**num.ind**) column with an estimated version of the total where it was not originally measured, which sums the numeric abundance of all species for each sample. The relative abundance (**rel.abun**) is then calculated using the estimated abundance divided by the total number of individuals.

For each individual sample, the **sample.depth** records the depth in the sediment from which the sample was taken; this is the mbsf (metres below sea floor depth) rather than the mcd (composite depth). The sample **age** provides the numeric age, whether from the original data or calculated using new age models, and the **age.err** indicates the precision of this estimate. The **segment** records where there were hiatuses in the sample, with separate age models being run for each segment. **Age.calc** indicates the type of age model used (orig, zone, magneto, interp, model). The age estimates from each of these different age models are also recorded separately. Original age, where the numeric age was already recorded, is indicated by an **age.calc** of “orig”, and no age model estimates. Zone ages were based on marker events both biostratigraphic and magnetostratigraphic. These are defined by the **zone**, with the **zon.age** being the mean of the **age.st** and **age.en**, and the range being given by **rng.age**. Interpolated ages (interp) use simple interpolations of these zonal markers by depth to give **int.age** and **err.int.age**. Where the models are based only on magnetostratigraphic age (magneto), the **mag.zone** indicates the markers, with the **mag.age** being the mean of **mag.age.st** and **mag.age.en**. The **int.mag.age** is the interpolation of these zonal markers, with the **err.int.mag.age** indicating the error in this estimate. The GAM (or linear model) estimate of the age is given by **mod.age**, with the r^2 (**r2**) of the model, and the number of points (**n.pts**) it is based on giving an indication of accuracy. The **age.model** identifies the original age model used in the datasets, e.g. which biostratigraphic zonation was used. When the age was already numeric, this was designated GTS2012 (updated to GTS2020). The type of events used to determine the age were also recorded (**AM.type**). Visual representations of these age models are available in the "Age models" file in the figshare data repository[18].

The **latitude** and **longitude** columns contain details about the sample site location, along with the current **water.depth** of the sample. Paleocoordinates (**pal.lat** and **pal.long**) were calculated using Matthews, et al. [35]. Where appropriate, ocean drilling program information, including the **leg**, **site**, **hole**, **core**, **section** and **sample.top** (in cm), were also recorded.

Differences in sampling strategy between sources introduces a possible source of bias. Therefore, where this information is available, sampling strategy was recorded. The **reason** indicates the purpose for which the data was originally collected: biostratigraphy, community analysis, proxies, selected species. This information will be useful for Triton users to determine whether the full dataset or only a subset is appropriate for their analysis. The **sample.type** indicates the method used to collect the sediment (e.g. piston core, box core). Sample **processing** details, when that information was available, records how the samples were processed, e.g., what sieve size was used, how many specimens were counted. The **preservation**, where it was recorded, gives an indication of whether thin-walled species are likely to be absent. **Trim** gives an indication of whether the record falls significantly outside the known range of the species and therefore should be included (inc) or excluded (exc) if trimming is used. The cut-off for the Neogene is 2 Ma outside the species known range, and 5 Ma for the Palaeogene. These are likely to be taxonomic misidentifications or the result of reworking.

The files and code required to run this dataset are provided in the figshare data repository[18]. The original stratigraphic events are provided in "Timescale conversion" and converted to the GTS 2020 dates using the "Ages" file. The species data is provided in "PF data". The original datasets are in "Triton data", and the intermediate stages of the data processing are provided in "Triton working". The code to create the final dataset ("Triton") is in the "Triton code" .zip file. The "Readme" file provides more details.

2.2.4 Technical Validation

The final Triton dataset contains 512,922 non-zero records, spread throughout the Cenozoic (Table 1). Neptune, the previous most complete dataset, contains 112,598 records. To put our dataset in context, the largest macrofossil dataset at an equivalent taxonomic level are bivalves in the Palaeobiology Database, with 197,606 records for the entire Phanerozoic as of November 2020, and only 79,427 for the Cenozoic. The full Triton dataset, including all the records where a species' abundance is recorded as zero, contains 1,716,087 records. These records derive from a range of sources (Fig. 1), which have different degrees of consistency in their structure and taxonomic data. For example, Pangaea data come from multiple different studies with many unique data structures.

Fig. 2 shows how the spread of records varies through time and with latitude (see also Table 1). Records are most dense in more recent time intervals due to the challenges of coring deeper sediments[40,41]. Record gaps can also result from lack of preserved calcareous sediment due to dissolution. For example, in the modern ocean, the mid-latitude Pacific is particularly lacking in calcareous sediments as are Neogene high latitudes, since the older bottom water found there is more acidic[42]. Practical limitations of obtaining samples can also influence sampling in high latitudes, which typically require relatively calm oceans and ice-free conditions for most of a cruise, helping to explain the relative lack of records above 60 degrees. Our efforts in this paper are concentrated on compiling Cenozoic data, because they are more plentiful and widespread than older data.

The full species list of Cenozoic planktonic foraminifera is obtained from Lamyman et al (in prep) and provided in "PFdata" in the figshare data repository[18]. When compared with this species list, our dataset contains records for 90% of valid species (394 of 438). Those species with no records tend to be recently identified (e.g. *Globoturborotalita paracancellata* which was described in Wade, et al. [26]), rarely used (e.g. *Turborotalia altispiroides* which was described in Bermúdez [43]) or actually rare (e.g. *Protentelloides dalhousiei*). For those species where there is at least one record, we can estimate the completeness of that record based on the fraction of age bins in which a species occurs between its speciation and extinction; 100% completeness implies that a species is found in every time bin of its expected range. Using 1 Ma bins, the median completeness for species is calculated to be 100% – 240 species (62.5%) having a ‘complete’ fossil record at that resolution. The mean completeness at this resolution is 87.8%. At the finer resolution of 0.5 Ma bins, 198 species (51.6%) have 100% completeness, while the mean is 83.4%. With this relatively high completeness level, plots of diversity through time (Fig. 3) indicate many of the major features of diversity change, such as the end Eocene extinctions at 34 Ma, are identified.

2.2.5 Usage Notes

The main version of the Triton dataset contains only the positive abundances. There is also a column (trim) that indicates whether species fall significantly outside their known ranges, which can be used to produce a trimmed dataset. However, this could potentially remove some samples that are true presences rather than reworking as a result of inaccurate speciation or extinction dates. As how to define the cut-off is a personal decision, the untrimmed version of the dataset is provided here. Additionally, speciation and extinction estimates might not be representative of the whole of a species’ geographical range, with many of these estimated based on subtropical zonal schemes (e.g. Wade, et al. [31]). Consequently, trimming is likely to be less precise for higher latitude sites, where regional speciation and extinction ages may differ, and the zonal age estimates themselves may be less accurate.

A dataset version including absences is also supplied, which has the potential to provide more detailed information about species distributions. However, the significance of absences depends on the scoring procedure of the original database. When foraminiferal distribution data is collected for community analyses, recording prescribed species abundances through time, species absence is more informative, than when foraminiferal analysis is focused only on biostratigraphic marker species. In the first case if a species was on the list and not recorded, it is likely it was searched for and not found, whereas in the second, an absence could imply it was not searched for. Absences for studies explicitly focussing on community analyses are more informative, and allow, for example, more precise studies of species climatological preferences.

Similarly, we urge caution when using this data for site level diversity studies. Where planktonic foraminifera were identified for purely biostratigraphic purposes, only a subset of species may have been searched for or studied. If those species lists/records are taken at face value, estimates of alpha diversity will be artificially low. Consequently, alpha diversity estimates should only be taken from studies (approximately 40% of the total dataset) that explicitly recorded the entire community. More comprehensive studies of diversity should focus on gamma diversity using binned ages and should account for spatial coverage.

The Triton dataset is provided as an open access resource with this paper[18]. When using it, we ask that you cite this paper. If a significant fraction of your data subset derives from ForCenS[21] or Neptune[14-16], we ask those papers are also cited.

Although this analysis aimed to target all the larger online sources of data for Triton there are inevitably some datasets which are not included, such as data tables from individual journal articles. By including the code used to reformat the Triton dataset, we aim to make sure that these datasets, and future research, can be added for further analyses. Additionally, updates to the ages of marker events or the taxonomy can be incorporated into Triton. As an example of how to update the taxonomy, we have included the updates from Lam and Leckie [29] and Lam and Leckie [32] (which are incorporated into Triton) as a separate file (Updated Taxonomy.xlsx[18]), and provide the code (Triton_Update.R[18]) to make these, or future, changes.

Code Availability

All the code used to generate this database is available in the TritonDB repository on github (https://github.com/IFenton/TritonDB), as well as in “Triton code” in the figshare data repository[18].

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Author contributions

IF, AW, ES, TA designed the project. IF and AW collected the raw datasets. AW downloaded and formatted the age models for the DSDP, ODP and IODP data. IF coded the database. TA provided expert advice on planktonic foraminiferal taxonomy and age models. DL, JR provided expert advice on planktonic foraminiferal databases. IF, AW, ES, TA drafted the manuscript, with input from DL, JR, AD, JY. All authors provided significant comments / feedback on the project.

Competing interests

We are not aware of any conflicts of interest in this project.

Tables

		Neptune	Triton	Percent Increase
Total		112,598	512,922	356%
Species	Macroperforate	102,466	474,876	363%
	Microperforate	10,132	38,046	276%
Period	Neogene	85,550	442,573	417%
	Paleogene	27,048	70,349	160%
Latitude	0-30°	60,315	297,135	393%
	30-60°	42,078	194,455	362%
	60-90°	4,231	21,332	404%
Abundance	Quantitative	8,899	229,045	2474%
	Semi-quantitative	82,752	228,802	176%
	Presence/absence	20,947	55,075	163%

Table 1. Summary statistics showing the data spread improvement of Triton compared to Neptune, the previous largest compilation of foraminiferal data.

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3. Ecological trends in pre-extinction geographic range trajectories of Cenozoic planktonic foraminifera

Abstract

The spatial distributions of living species are being impacted by the ongoing effects of anthropogenic climate forcing. As such, there is a need to quantify potential patterns within modern biodiversity that may allude to imminent extinction, especially within ecosystems critical to a sustainable future. The oceans are comparatively understudied in terms of biodiversity and conservation, therefore, to identify and assess the presence of any potential geographic pre-extinction patterns within marine organisms, the marine micropalaeontological record is examined. Here, open ocean sedimentary archives exceptionally preserve ancient climate perturbations of comparable magnitude to the predicted impacts of future warming projections. The Cenozoic planktonic foraminifera are of particular value as they have the best-preserved species-level fossil record of the last 66 million years, which is complimented by recent efforts that have produced an occurrence database, Triton, with over half a million individual occurrence records. With this novel dataset, global geographic pre-extinction patterns within the Cenozoic planktonic foraminifera are found to document a near consistent decline in geographic range approaching extinction. However, species which evolved in environments inherently subject to greater abiotic variability may potentially show resilience against negative abiotic effects and selection pressures, expanding their geographic range until they are ultimately ecologically overwhelmed and go extinct. When analysing rapid climate events (< 1 Myr) throughout the Cenozoic, the most geologically rapid have the greatest impact on geographic range declines. As such, future consequences of warming scenarios have the potential to trigger large scale changes to the structure of oceanic biodiversity due to geographic range reductions in plankton communities. Continued monitoring of populations that characterise basal trophic systems will be necessary to identify impending ecosystem collapse.

3.1 Introduction

The fossil record is a rich and direct source of information for studying the history of life on Earth, and much attention has been given to understanding how trends and patterns observed from past biodiversity may help us make better predictions about how biodiversity in modern ecosystems might respond to rapid climate change. Efforts in recent years have sought to examine the palaeontological record to quantify the potential ecological (Alroy, 2008; Wade et al. 2008; Gilman et al. 2012; Cahill et al. 2012; Urban et al. 2012; Edgar et al. 2013a; Si & Aubry, 2018; Fox et al. 2020; Todd et al. 2020; Shaw et al. 2021; Woodhouse et al. 2021), morphological (Witting, 1997; Knappertsbusch, 2007; Wade & Olsson, 2009; Wade & Twitchett, 2009; Weinkauf et al. 2014, 2019; Falzioni et al. 2018; Brombacher et al. 2017a; Atkinson et al. 2019), and geographic patterns (Jenkins, 1992; Foote, 2003, 2007, 2014, 2016; Foote et al. 2007, 2008, 2016; Liow & Stenseth, 2007; Liow et al. 2010; Harnik et al. 2012; Finnegan et al. 2015; Hull et al. 2015; Urban, 2015; Stanton et al. 2015; Kiessling & Kocsis, 2016; Jonkers et al. 2019; Smits & Finnegan, 2019) which may act as indicators of extinction risk within ancient life.

Amongst the numerous fossil taxa available for palaeontological analyses the calcareous marine microplankton, specifically the macroperforate planktonic foraminifera, are an ideal study system for investigating extinction dynamics in the past. These organisms have the most well-studied species level fossil record of any group throughout the Cenozoic (Aze et al. 2011; Fordham et al. 2018; Lamyman et al. in prep.), a mature taxonomy and robust phylogeny (e.g., Olsson et al. 1999; Pearson et al. 2006; Aze et al. 2011; Wade et al. 2018), and they are extensively sampled from the marine sediment record, which often allows for excellent age control of species ranges through time (Fenton and Woodhouse et al. 2021). Additionally, the group preserve a full body fossil that records ambient water chemistry, allowing us to investigate both their morphological and ecological evolution through time and how they can be influenced by climate trends and geologically-abrupt events in the rock record (e.g. Kelly et al. 1996; Pearson et al. 2001; Zachos et al. 2001; Schmidt et al. 2004a, b; Liow et al. 2010; Ezard et al. 2011; Hönisch et al. 2012; Peters et al. 2013; Fraass et al. 2015; Lowery & Fraass, 2019; Tucker et al. 2019; Lowery et al. 2020; Boscolo-Galazzo et al. 2021; Brombacher et al. 2021).

The utility of this group for geographic and temporal analyses has been further enhanced by the production of several micropalaeontological occurrence datasets (Lazarus, 1994; Spencer-Cervato, 1999; Diepenbroek et al. 2002; Siccha & Kučera, 2017; Renaudie et al. 2020). The most recent effort, the Triton dataset, has compiled all Cenozoic planktonic foraminiferal occurrence datasets with many new deep time records (Fenton & Woodhouse et al. 2021). Triton now represents the largest group-specific fossil occurrence dataset ever created and permits the inspection of geographic patterns within the planktonic foraminiferal record at a greater resolution than ever before. Recent work investigating the factors that influence extinction probability in marine plankton highlighted the opportunity planktonic foraminifera present for unpacking the influence of ecology on the geographic range histories of species, which has largely been untested to date (Smit and Finnegan, 2019).

In this study, Cenozoic planktonic foraminiferal distribution data in Triton has been assessed using linear models to determine whether background climate state (“Greenhouse” or “Icehouse”, e.g., Westerhold et al. 2020) or ecological affinity influences the geographic distributions of species prior to extinction (in this study the final third of a species stratigraphic range). In addition, species pre-extinction geographic range trajectories during four major global-scale climatic perturbations are compared against the background trends of the last 66 Myrs. Using the newly constructed Triton dataset (Fenton & Woodhouse et al. 2021), model results indicate that the ecological affinity of Cenozoic planktonic foraminiferal species can influence the rate of geographic range contraction in the final third of species ranges and that rapid climate change events can also have a significant impact, but not in all cases studied.

3.2 Methods

The Triton dataset (Fenton & Woodhouse et al. 2021) was downloaded, and all macroperforate planktonic foraminiferal species were assigned speciation and extinction datums in accordance with Aze et al. (2011) and Lamyman et al. (in. prep) and binned into 88-time bins with equal length (0.75 Myrs). This bin length was chosen as it allowed for higher resolution sampling than 1 Myr time bins, but still captured sufficient data per bin in the more sample deficient parts of the records in the early Cenozoic (Figure 1). All extant species (see Schiebel & Hemleben, 2017), and species which exhibit extinction in the youngest Cenozoic time bin (0-0.75 Ma) were removed, due to the addition of sediment trap and shallow coring data included within Triton which results in a ~10-fold increase in sampling intensity in this final time bin (Figure 1). Additionally, all species occurrences located outside of the assigned stratigraphic ranges were removed to eliminate much of the occurrence data likely attributable to misidentification and/or reworking which may create artificial “tails” within speciation and extinction data (Liow et al. 2010).

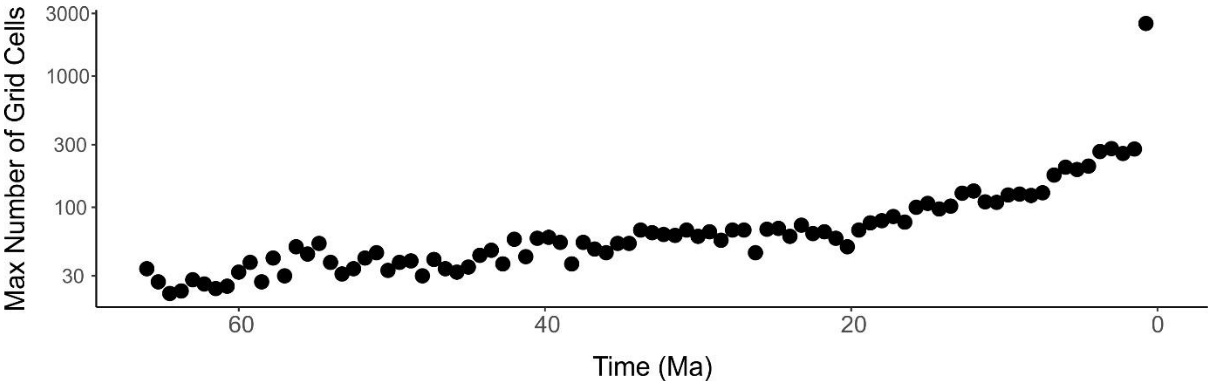

Figure 1. The maximum number of grid cells available per 0.75 Myr time bin which contain planktonic foraminifera in Triton (Fenton & Woodhouse et al. 2021). Note that the y-axis scale is logarithmic.

To assess changes in geographic range prior to extinction, the “raster” package (Hijmans, 2020) in R software (R Core Team, 2020) was used to assign all macroperforate planktonic foraminiferal palaeolatitudinal and palaeolongitudinal data in Triton (Fenton & Woodhouse et al. 2021) into grid cells with coordinate dimensions of 1 x 1 latitudinal and longitudinal decimal degrees. Only the final third of each species range was used for analysis and any species which exhibited less than five total time bins of occurrence across their range were removed from the study as a third would yield less than two occurrence bins. Species with stratigraphic ranges spanning more than five-time bins which had bins lacking occurrences within the final third of their range were also omitted from further analyses. The trimming of taxa resulted in the removal of 170 species from the original dataset, with 168 remaining for analyses. Of these remaining taxa, 96 originate in the "Greenhouse" regime (66 – 33.9 Ma), and 72 within the "Icehouse" (33.9 – 0 Ma).

As species stratigraphic ranges differ from one another, and the number of occupiable grid cells within Triton generally increases through the Cenozoic (Figure 1), the final third of each species range was scaled to allow for proportional comparison (collective final third mean = 2.96, and standard deviation = 2.12). Each species stratigraphic range was calculated and scaled from 66% - 100%, with 66 % representing the initiation time of the final third, and 100% representing the point of extinction. Additionally, each species' minimum and maximum quantity of occupied grid cells from their entire stratigraphic range were scaled from 0-1.

Once grid cell values were generated, linear models were produced in R software (R Core Team, 2020) and the slope of the regression line was used to determine the rate of species geographic range decline throughout the final third of each species stratigraphic range (see Figure 2 for biogeographic range contraction example). These regression values were presented as mean values for all species across the whole Cenozoic and also as subdivided groups that allowed the relationship between the rate of decline and climate regime during speciation, climate perturbations, and ecological habits to be assessed. To examine whether the climatic regime at the time of speciation influenced pre-extinction trajectories, all species which evolved prior to the start of the Oligocene (~33.9 Ma) were assigned to the Greenhouse climate regime and those that speciated afterwards to the Icehouse (e.g., Westerhold et al. 2020). Furthermore, to determine whether species ecology plays a role in the rate of geographic decline all species were assigned to their respective "ecogroups" which represent where species lived within the water column and whether they hosted algal photosymbionts

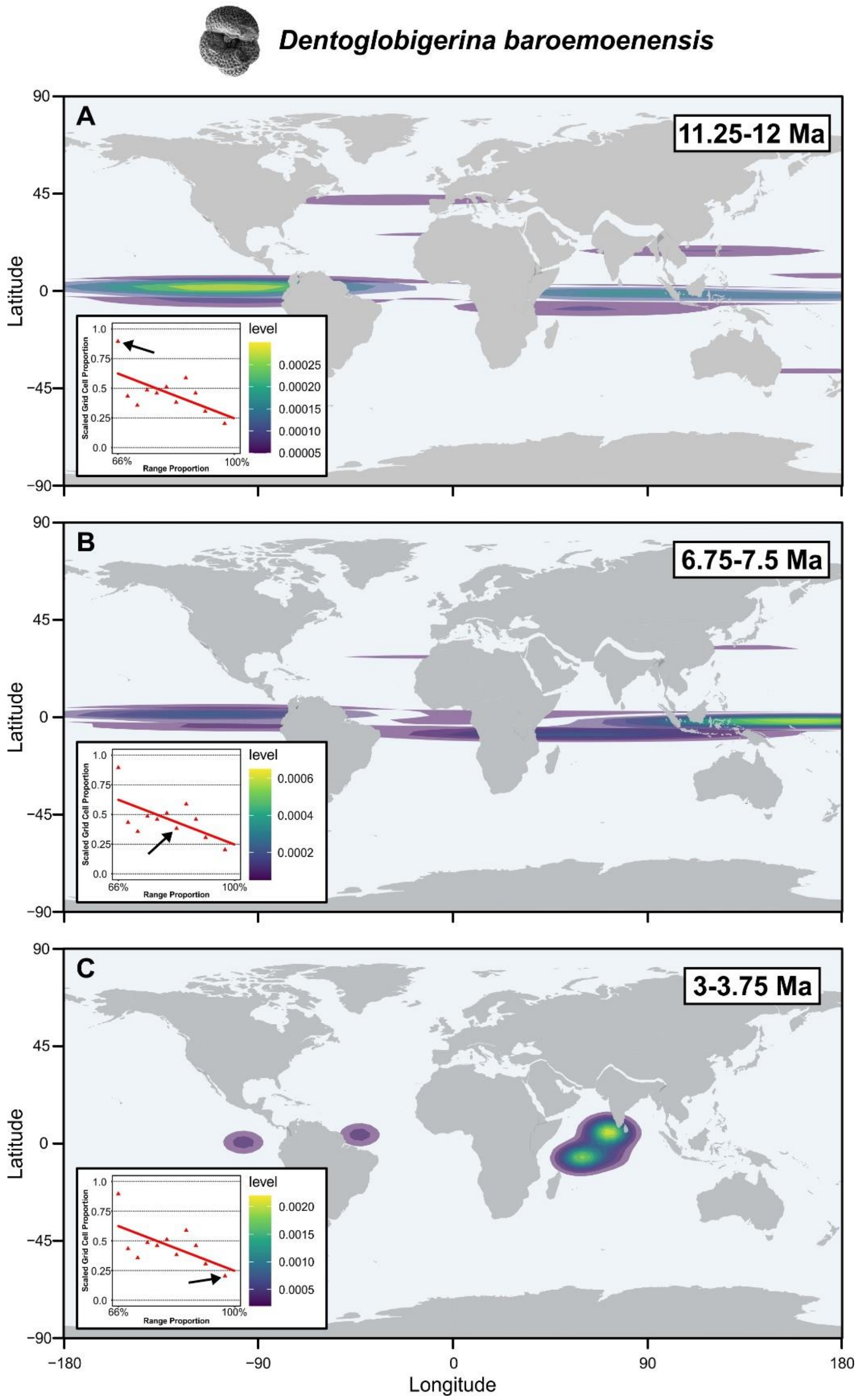

Figure 2. Selected time-bins showing the contracting biogeographic density distribution of *Dentoglobigerina baroemoenensis* in the final third of its stratigraphic range. A, 11.25-12 Ma – species is most prominent in the east equatorial Pacific Ocean and occupies palaeolatitudes 45° N and S of the equator, B, 6.75-7.5 Ma – species is most concentrated in the west equatorial Pacific Ocean, palaeolatitudinal range is contracted and species is lost from the southern hemisphere extratropics, C, 3-3.75 Ma – species is most proliferent in the tropical Indian Ocean, almost entirely absent in other ocean basins. Plate reconstructions based on Seton et al. (2012).

(Aze et al. 2011). These are defined as: ecogroup 1 = surface mixed layer dweller with photosymbionts, ecogroup 2 = surface mixed layer dweller without photosymbionts, ecogroup 3 = thermocline dweller, ecogroup 4 = subthermocline dweller. Additionally, four major climatic events during the Cenozoic were investigated; the Paleocene-Eocene Thermal Maximum (PETM, ~56 Ma), Middle Eocene Climatic Optimum (MECO, ~40 Ma), the Eocene-Oligocene Boundary (EOB, ~34 Ma), and the Intensification of Northern Hemisphere Glaciation (INHG, ~3 Ma), grouping taxa which underwent extinction within 1 Myr of these events to assess how species respond geographically to global-scale climate perturbations (Westerhold et al. 2020). Finally, species with extinctions that have historically been used as biostratigraphic datums (Wade et al. 2011) were identified to investigate whether species geographic range trajectories are influenced by sampling efforts, which could be the case if taxa are systematically more regularly recorded near to their extinction interval in Triton due to their use as a biostratigraphic zone marker.

3.2.1 Statistical analysis and modelling extinction trajectories

Mann-Whitney U (MWU) tests were performed for each of the assigned ecogroups against all other species across the entire Cenozoic, and across the two prevailing climate regimes throughout the Cenozoic (Greenhouse 66 – 33.9 Ma and Icehouse 33.8 – recent) to assess whether specific planktonic foraminiferal ecogroups showed regression slopes which differed significantly from all others. MWU tests were repeated for each of the four climatic events to determine whether species which underwent extinction within 1 Myrs of these events had regression slopes significantly different from the Cenozoic background values and the background values of the prevailing climate regime at the time the events took place (Greenhouse for PETM, MECO and EOB, and Icehouse for INHG).

The underlying *climate regime*, *ecogroup*, *time of extinction*, *stratigraphic range*, and *biostratigraphic utility* of each species were used to predict the regression slope values within the final third of species ranges with a generalized least squares (GLS) model fitted in R software (R Core Team, 2021) using the package ‘nlme’ (Pinheiro et al. 2020). The best fitting model was evaluated using the Akaike Information Criterion (AICc). Model fitting was achieved by systematically dropping each explanatory variable and comparing model AICc values to determine whether the dropped term improved model performance (Zuur et al. 2009). The best fitting models required no fixed variance structure.

3.3 Results

Linear model results indicate that all groups show a mean range decline throughout the Cenozoic, Greenhouse, and Icehouse (Table 1). All data treatment has negative slope values, although there is variation in the gradient of these average trends. The mean value of geographic range decline is steeper amongst species that originated in the Greenhouse climate regime than they are for the whole Cenozoic or the Icehouse (Table 1 and Figure 3). When considering the whole Cenozoic, MWU test results indicate that the subthermocline ecogroup is the only ecogroup that is statistically significantly different from background values, however this significance is not maintained when filtered by Greenhouse or Icehouse regime. The shallowest rates of range decline are seen in photosymbiotic mixed layer taxa in the Icehouse (slope -0.106).

	Cenozoic (slope)	**Cenozoic (*p* value)**	**Greenhouse (slope)**	**Greenhouse (*p* value)**	**Icehouse (slope)**	**Icehouse (*p* value)**
All	-0.473	-	-0.528	0.3824	-0.410	0.3824
Photosymbiotic mixed layer	-0.437	0.4557	-0.582	0.9873	-0.106	0.5199
Asymbiotic mixed layer	-0.566	0.7626	-0.488	0.7013	-0.716	0.9913
Thermocline	-0.449	0.3512	-0.510	0.6929	-0.492	0.1774
Subthermocline	-0.645	***0.009614***	-0.839	0.2046	-0.628	0.05103

Table 1. Mean slope values for all species across the whole Cenozoic and within each climate regime (Greenhouse and Icehouse). Mean slope values are also presented for subsets of the data where species are assigned to one of four different ecological groups (photosymbiotic mixed layer, asymbiotic mixed layer, thermocline and subthermocline). Mann-Whitney U tests were performed to identify where ecogroup subsets were statistically significantly different from the total population for the three-time intervals and the results are presented as *p* values, with bold, italicised values indicating where populations are significantly different.

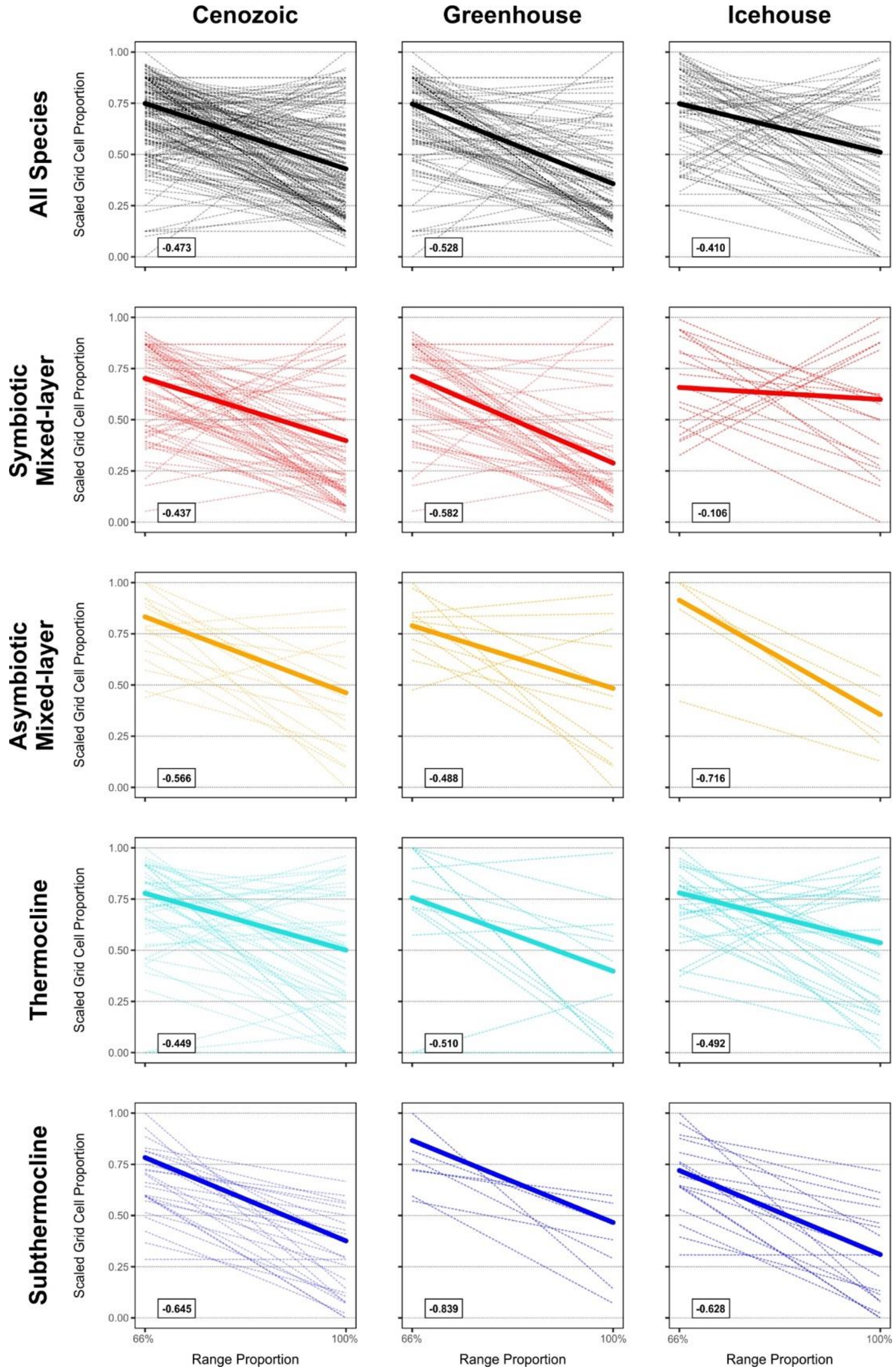

Figure 3. Panels show the linear regression results for species range trajectories as scaled grid cell proportions in the final third of their ranges (66 – 100%). Faint, dashed lines represent individual species trajectories and bold lines represent mean values. Mean slope values for each grouping are shown as an insert in each panel. Species ranges are presented for the whole Cenozoic and for each climate regime (Greenhouse and Icehouse) and as subsets where species are assigned to one of four ecological groups (photosymbiotic mixed layer, asymbiotic mixed layer, thermocline and subthermocline).

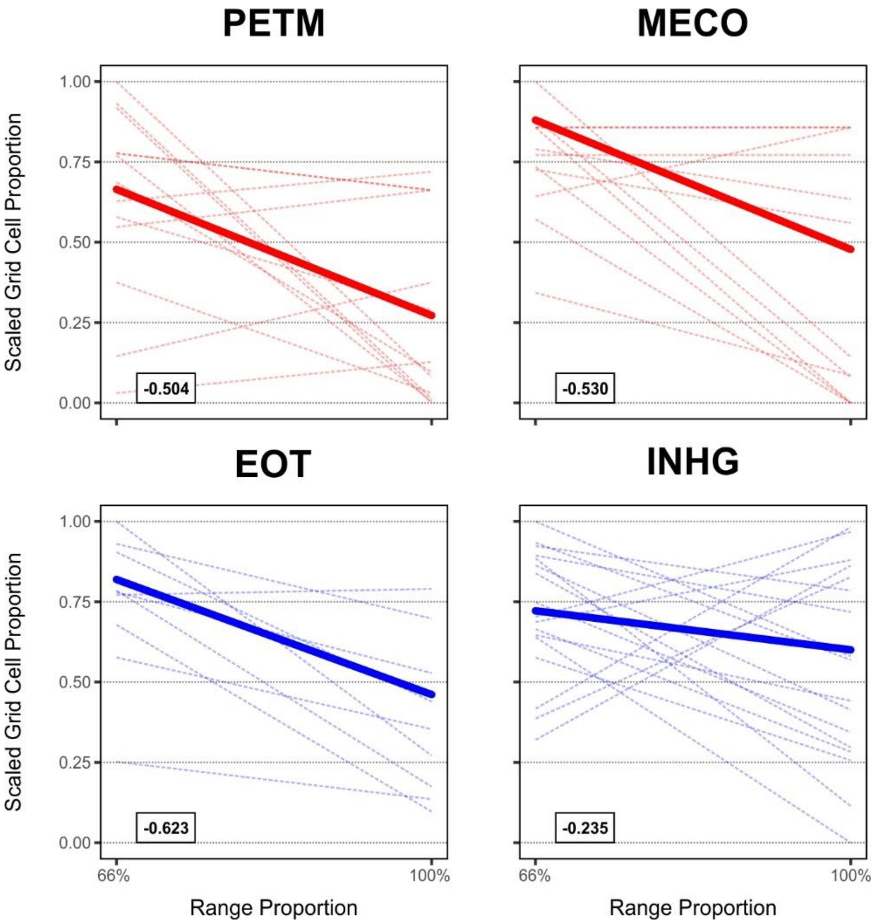

Figure 4. Panels show the linear regression results for species range trajectories as scaled grid cell proportions in the final third of their ranges (66 – 100%). Faint, dashed lines represent individual species trajectories and bold lines represent mean values. Mean slope values for each grouping are shown as an insert in each panel. The panels represent species trajectories across four climate events throughout the Cenozoic, the Paleocene-Eocene Thermal Maximum (PETM, ~56 Ma), Middle Eocene Climatic Optimum (MECO, ~40 Ma), the Eocene-Oligocene Boundary (EOB ~34 Ma), and the Intensification of Northern Hemisphere Glaciation (INHG, ~3 Ma).

	PETM	MECO	EOB	INHG
Slope	-0.504	-0.530	-0.623	-0.235
Cenozoic (*p* value)	***0.04464***	0.5807	0.319	0.4797
Regime (*p* value)	***0.04241***	0.7497	0.2114	0.2875

Table 2. Mean slope values for species across four climate events throughout the Cenozoic, the Paleocene-Eocene Thermal Maximum (PETM, ~56 Ma), Middle Eocene Climatic Optimum (MECO, ~40 Ma), the Eocene-Oligocene Boundary (EOB ~34 Ma), and the Intensification of Northern Hemisphere Glaciation (INHG, ~3 Ma). Mann-Whitney U tests were performed to identify where events are statistically significantly different from the whole Cenozoic and the climate regime they occurred in (“Greenhouse” for PETM, MECO and EOB, and “Icehouse” for INHG), and are presented as *p* values, with bold, italicised values indicating where populations are significantly different.

Linear model and MWU test results investigating the mean pre-extinction geographic range declines within proximity to the four global-scale climatic perturbations indicate that the range declines during the PETM were statistically significantly different from background values when considered against both the whole Cenozoic and the prevailing climate regime (Table 2 & Figure 4). The shallowest rates of range decline are seen in the INHG interval (slope -0.235), although this is not statistically significant.

Model	**Parameters**	**AICc**
Full model	Regime, ecogroup, biostratigraphic marker, end, range	680.9029
Best model	Biostratigraphic marker, end, range	680.1976

Table 3. Summary of GLS multiple regression analysis showing the full and best models for predicting the regression slope for extinction.

Response	**Parameters**	**Value**	**SE**	**t**	***p***
Geographic range trajectory	Biostrat. marker	0.5322162	0.3212723	1.656589	0.0996
	Extinction age	0.0198668	0.0084280	2.357222	***0.0196***
	Range	0.0626585	0.0247046	2.536311	***0.0122***

Table 4. Summary of best fitting GLS multiple regression model for predicting the regression slope for extinction. Bold and italicized p-values values are statistically significant ($p < 0.05$).

The linear regression slopes of individual species (Figure 3) show a general trend for species range declines in the final third of their stratigraphic ranges for most species, as evidenced by mean negative values for all data treatments, however some species show increasing geographic range in the final third of their stratigraphic range, this is true for all ecogroups except for subthermocline taxa which consistently have negative slope values (Table 1; Figure 3). Additionally, individual species slope intercepts on the vertical axis are rarely at 1.00 at the time of initiation of the final third indicating that many species were already reduced from their previous maximum geographic range prior to the final third of their stratigraphic range.

Model fitting shows that a combination of the parameters *time of extinction*, *stratigraphic range*, and *biostratigraphic utility* provide the best model for predicting the slope of extinction trajectories (Table 3), and of these three variables an *extinction date* earlier in the Cenozoic, and a longer species *stratigraphic range* are statistically significantly correlated with more positive geographic ranges trajectories prior to extinction.

3.4 Discussion

3.4.1 Cenozoic extinction trajectories

Throughout the Cenozoic the majority of species show a geographic range decline prior to extinction. Although range expansion is also seen, this is true for all ecogroups with the exception of the subthermocline ecogroup, the deepest-dwelling taxa, which are the only Cenozoic ecogroup to exhibit consistent geographic range decline prior to their extinction (Figure 3). In the open ocean, water temperature, salinity, radiation, turbidity, abundance of prey, and trophic demands become less variable with depth (Schiebel & Hemleben, 2017), hence environmental conditions are typically more stable at depth’s beyond 100m than they are in the surface mixed layer on timescales applicable to planktonic foraminifera life cycles (Birch et al. 2013; Toffoli & Bitner-Gregersen, 2017). As such, species living in the surface mixed layer are better adapted to more variable environmental conditions (Schiebel & Hemleben, 2017). The consistently negative geographic range trajectories amongst subthermocline dwellers may be associated with the reduced environmental variability with water column depth and its potential role within their phylogenetic history. Greater environmental variability during the early evolutionary development of species is posited to promote lasting resilience against abiotic selection pressures (Liow et al. 2010). Therefore, phenotypic plasticity borne from the habitat of speciation may permit certain planktonic foraminifera the ability to produce exaptations or geologically rapid within-clade character changes when subjected to environmental selection pressures (Gould & Vrba, 1982; Williams, 1992; West-Eberhard, 2003). The observation that subthermocline taxa exhibit geographic ranges that “dwindle down”, rather than the generally more rapid declines shown by other ecogroups (Figure 3), may reflect a reduced ability to mitigate harmful selection pressures leading up to their extinction due to reduced rates of environmental change within the subthermocline.

3.4.2 Regime extinction trajectories

Though no ecogroups were significantly different from one another within the two different climate regimes (Table 1), Greenhouse species on the whole tended to have steeper slopes of geographic range decline (Figure 3, Table 1). The clear-cut exception to this pattern is observed within photosymbiotic mixed layer dwellers hailing from the Icehouse regime (Figure 3), where several species with notably positive regression slopes influence the mean ecogroup signal to appear almost flat (Figure 3). However, there are examples within both climate regimes of positive regression slopes for species within all ecogroups, barring the subthermocline taxa (Figure 3).

The fact that several Icehouse photosymbiotic mixed layer dwellers exhibit a rise in geographic range prior to extinction (Figure 3) may suggest that some species housing photosynthetic algal symbionts (Aze et al. 2011) undergo geologically rapid (< 0.75 Myr) extinction from the peak of their geographic range. Why some species of this ecological habit would exhibit this pattern whilst others do not is perplexing. All five taxa identified that show this trend are from phylogenetically distinct genera (Supplementary Data; Aze et al. 2011.), with the exception of the ancestor-descendent pair *Dentoglobigerina globosa* and *Dentoglobigerina altispira* (Wade et al. 2018). Furthermore, new research indicates that multiple extant species which occupy the thermocline are observed to have obligate and/or facultative photosymbiosis (Schiebel & Hemleben, 2017; Takagi et al. 2019). In light of these findings, the examination of the Icehouse thermocline species within this study which also exhibit positive regression slopes (Figure 3) reveals that all of these species currently have living descendants/sister taxa observed or inferred to exhibit photosymbiosis (Faber et al. 1989; Hemleben et al. 1989; Aze et al. 2011; Schiebel & Hemleben, 2017; Takagi et al. 2019).

Modern planktonic foraminifera can host a variety of algal photosymbionts hailing from multiples discrete phylogenies (Hemleben et al. 1989; Schiebel & Hemleben, 2017; Gaskell & Hull, 2019; Takagi et al. 2019), and this capacity to implement a wide spectrum of photosymbiotic associations may provide photosymbiont-hosting species a range of ecological mechanisms with which to enhance their nutritional flexibility with only minimal metabolic adaptation (Stoecker er al. 2009; Takagi et al. 2019; Woodhouse et al. 2021). Though clearly not consistent across all photosymbiotic planktonic foraminifera (Figure 3), the geologically rapid (< 0.75 Myr) geographic range reductions suggested by the positive regression slopes amongst these forms may be interpreted to represent heightened ecological resilience up until the point of extinction, which is not replicated within other ecogroups. Unlike subthermocline dwellers, species which have evolved within the more environmentally heterogenous shallower waters are potentially better ecologically preconditioned to withstand rapid abiotic changes which may prove more detrimental to deeper dwellers (Figure 3).

Ecological preconditioning, niche habit flexibility, and photosymbiosis may therefore better equip species to withstand environmental selection pressures with little to no geographic range detriment until such pressures surpass a threshold (Figure 3). Eventually, environmental changes detrimental to ecological functioning would either culminate or periodically cycle to increase extinction risk and outpace adaptive responses or exaptations that could mitigate abiotic pressures as species are ultimately driven to extinction (Gould & Vrba, 1982; Harvey & Pagel, 1991; Williams, 1992). Further research is clearly required to characterise the ecological features and phenotypes which allow certain species to endure environmental conditions far-removed from where they evolved, however, the quantification of such biodiversity metrics is vital for the future preservation of modern phylogenetic diversity as the planet shifts towards an ecologically unfamiliar climate regime (Cantalapiedra et al. 2019).

Steepened extinction trajectories within Icehouse asymbiotic mixed layer dwellers (Figure 3; Table 1) which occupy the same depth habits as their potentially more resilient photosymbiont-hosting kin may further support these hypotheses. Where photosymbiont-hosting forms may be able to exploit a variety of photosymbiotic relationships to prolong their geographic range maxima, asymbiotic Icehouse species express a consistent loss of geographic range prior to extinction (Figure 3). The entire group show geographic range trajectories which, like the subthermocline taxa, “dwindle down”, though at a faster rate than the deeper dwelling forms which may be due to the greater environmental variability present in the mixed layer (Figure 3; Table 1). Nevertheless, sharing the same habitat as photosymbiont-bearers would likely subject these species to the same selection pressures, and the prolonged linear declines within asymbiotic forms may indicate less successful mitigation of the selection pressures which photosymbiotic species might withstand more easily.

These observed patterns lend their support to previous studies, where heightened environmental variability during the early evolutionary development of species may promote ecological resilience (Liow et al. 2010 and Chapter 3 herein). Additionally, recorded pre-extinction morphological and geochemical responses seen in multiple mixed layer Cenozoic planktonic foraminifera potentially demonstrates their ability to respond more flexibly to abiotic pressures (Wade et al. 2008; Wade & Olsson, 2009; Edgar et al. 2013a; Si & Aubry, 2018; Shaw et al. 2021; Woodhouse et al. 2021). If these inferences prove correct, recognising pre-extinction patterns in modern planktonic foraminifera populations experiencing heightened extinction risk may be dependent upon the ecology and depth habitat of the species in question.

Pre-extinction patterns of species that originated in the Icehouse are not matched by taxa which originated in the Greenhouse (Table 1 & Figure 3), with notably fewer steeply positive geographic range trajectories exhibited across ecogroups. In contrast with the Icehouse, geographic range expansion prior to extinction is observed within all other ecogroups than the subthermocline (Figure 3), and if the relationships observed within the Icehouse are consistent, positive regression slopes amongst thermocline dwellers in the

Greenhouse may in fact identify extinct lineages housing photosynthetic algae (Takagi et al. 2019). Photosymbiotic forms in the Greenhouse exhibit markedly more negative regression slopes than their Icehouse equivalents (Figure 3). Functional differences in photosymbiont-hosting (Gaskell & Hull, 2019), coupled with the comparatively more homogeneous water column structure of the Greenhouse ocean (Sexton et al. 2006; Cramer et al. 2009, 2011; Norris et al. 2013) may have limited the ecological flexibility of this niche habit at this time (Stoecker et al. 2009; Takagi et al. 2019; Woodhouse et al. 2021). The severe loss of photosymbiont-hosting taxa across the EOB and during the descent into the Icehouse may be further indication of their ecological shortcomings during this regime (Aze et al. 2011; Ezard et al. 2011; Inglis et al. 2015).

3.4.3 Cenozoic climatic perturbation extinction patterns

Amongst the four climate events analysed, only the PETM, the most significant hyperthermal of the Cenozoic (Foster et al. 2018), is identified to be statistically significantly different from both the Cenozoic and the background climate regime (Figure 4; Table 2). The most severe Palaeozoic and Mesozoic hyperthermals are notably marked by dramatic changes in global biodiversity, however despite evolving during the Jurassic, planktonic foraminiferal species richness appears to have responded negatively to Oceanic Anoxic Event 1b (OAE1b) (Jenkyns, 2010; Foster et al. 2018; Kump, 2018; Lowery et al. 2020). The early Paleogene hyperthermals, though associated with potentially thermally prohibitive temperatures and ocean acidification, resulted in severe extinction within only benthic foraminifera (Thomas, 1989; Thomas & Monechi, 2007; Schmidt et al. 2018), generating only minor changes to planktonic foraminiferal species richness (Aze et al. 2011; Ezard et al. 2011; Fraass et al. 2015; Arimoto et al. 2020; Lowery et al. 2020). It is therefore likely that the statistical significance of the extinction trajectories during the PETM may reflect rapid turnover, within which species “extinctions” actually represent pseudoextinction (Aze et al. 2011).

Significant changes in the structure and circulation of the global water column are the most noteworthy drivers of extinction in the planktonic foraminifera (D’Hondt et al. 1998; Leckie et al. 2002; Henehan et al. 2019; Lowery et al. 2020), and the two major Cenozoic cooling events, the EOB & INHG, are intrinsically linked to stepwise dramatic expansion of continental-scale icesheets. These important phases in the development of the cryosphere were accompanied by intensified flow of global mode waters, upwelling of cool, nutrient-rich bottom waters, a substantial steepening of vertical and latitudinal marine temperature gradients, and a reduction in global particulate organic carbon remineralization and oxygen minimum zone intensity (Coxall et al. 2005; Edgar et al. 2007; Liu et al. 2009; Pälike et al. 2012; Villa et al. 2014; Goldner et al. 2014; Sarkar et al. 2019; Zhang et al. 2019; O'Brien et al. 2020; Hayashi et al. 2020; Boscolo-Galazzo et al. 2021; Hutchinson et al. 2021). These features have come to typify the bipolar Icehouse climate of the Recent and their ecological effects are potential mechanisms for the substantial geographic range reductions and extinctions documented across these two cooling events (Figure 4; Table 2).

At face value, the planktonic foraminiferal fossil record would appear to indicate that the associated environmental effects of anthropogenic climate change; warming, acidification, and hypoxia (e.g., Tyrell, 2008; Doney et al. 2009; Boscolo-Galazzo et al. 2013; Penman et al. 2014; Ito et al. 2017; Remmelzwaal et al. 2019; Fox et al. 2020; Henehan et al. 2020) would have little effect upon the biodiversity of the modern planktonic foraminifera. However, the rates of environmental change associated with modern climate change are unprecedented in the past 66 Myrs (Barnosky et al. 2011; Kolbert, 2014; Ceballos et al. 2015). A potential warming event of the current magnitude could melt modern continental-scale ice sheets, which hold the meltwater potential to dramatically disrupt global ocean circulation patterns, nutrient distributions, and water column structure, all of which are known to have significant historical impacts on planktonic foraminiferal diversity (Sherwood & Huber, 2010; Hu et al. 2011; Rhein et al. 2013; Purich et al. 2018; Zika et al. 2018; Bindoff et al. 2019; Golledge et al. 2019; Asseng et al. 2021).

3.4.4 Considerations and prospects

Model results (Table 3) that provided the strongest explanatory support for species ranges trajectories prior to extinction included *extinction age*, species *stratigraphic range* and whether a species extinction is used as a *biostratigraphic marker* in Wade et al. (2011). Of these three variables only *extinction age* and species *stratigraphic range* are independently statistically significant (Table 4). The lack of independent statistical significance of *biostratigraphic marker* species status within the best fitting model would suggest that, in spite of being useful for stratigraphic correlation and potentially preferentially sought out by biostratigraphers, marker species occurrences do not seem to be recorded at a higher rate prior to extinction.

Model results (Tables 3 and 4) indicate that species which go extinct earlier in the Cenozoic tend to show more positive geographic range trajectories prior to extinction, typically going extinct when they are closer to their maximum geographic range. The early Cenozoic record in particular is typified by higher rates of planktonic foraminiferal turnover and shorter species ranges, typical of an “early burst” model following the K-Pg extinction (Ezard et al. 2011). Due to the fact the sampling intensity increases in the later part of the Cenozoic ~20 Ma – Recent (Figure 1) it would suggest that this signal is not entirely a function of sampling bias.

However, there is clearly complexity in the record that is not picked up by these analyses due to the nature of the methodological approach. Occurrence data was binned into 0.75 Myr length time bins and species with very short stratigraphic ranges (occurring in less than 5-time bins), and those that had gaps in the final third of their stratigraphic ranges, were excluded. This filtering has removed 50.3% of shorter ranging and poorly represented species, as such the range trajectories of these taxa are not represented in these analyses and may include patterns unique to shorter ranging and rarer taxa. Additionally, the linear modelling approach in this work may also obscure some of the complexity associated with species range trajectories. The use of more complex modelling techniques, and higher-resolution analysis through more rigorously sampled and accurately dated sections of the Cenozoic such as the Quaternary (Lisiecki & Raymo, 2005; Spratt & Lisieceki, 2016), will provide more rigorous insights into Cenozoic planktonic foraminiferal pre-extinction geographic range trajectory dynamics.

3.5 Conclusions

Cenozoic planktonic foraminiferal extinction trajectories suggest that species which evolved in environments inherently subject to higher abiotic variability and that host photosymbionts may exhibit greater resilience against selection pressures. The pre-extinction trajectories within these species indicate potential adaptive resilience to selection pressures prior to the culmination of threshold values, which allows species to better maintain their geographic ranges up to the point of extinction. Assessments of the extinction trajectories of planktonic foraminifera across major climatic perturbations suggest more rapid events, e.g., the PETM have the most significant impact on geographic range reductions. Despite relatively muted extinction rates across geological hyperthermals, the oceanic knock-on effects of anthropogenic warming on the Icehouse cryosphere and the rapid rates of change will likely increase future extinction risk and geographic range declines with plankton communities in the marine realm.

4. Climate regime drove spatial patterns in speciation and dispersal dynamics of planktonic foraminifera

Abstract

The marine microfossil record of Cenozoic planktonic foraminifera is the most complete and phylogenetically resolved of any group of organisms available for study, and there have been substantial efforts to collate global occurrences and utilise this wealth of data in macroevolutionary studies. As such, the novel planktonic foraminiferal occurrence database, Triton, is used to assess the biogeographic variability of this group through geological time, examining trends in speciation and extinction locales. It is found that palaeolatitudes of speciation and extinction varied with regard to the underlying global climate conditions of the time. The Greenhouse regime of the early Paleogene was dominated by extratropical speciation locales which, as global temperatures declined, were progressively complimented by lower latitude speciation. This tropical speciation cradle acts as the primary marine palaeolatitudinal cradle in the cooler climates of the Icehouse regime and modern day. The global biogeographic patterns observed within this study reveal fundamental elements of marine macroevolutionary dynamics through geological time, suggesting that the locations of taxon speciation and extinction are driven primarily by the underlying global temperature. As anthropogenic forcing pushes global climate towards a state potentially analogous to the Greenhouse world of the Paleogene, marine speciation and latitudinal biodiversity dynamics may migrate to higher latitudes, altering future marine ecosystem function.

4.1 Introduction

Determining the mechanistic drivers of speciation and extinction are core to our understanding of how life evolves and its resiliency to climate change, and resolving these processes, in particular their spatial dynamics, is increasingly pertinent given the current biodiversity crisis (Barnosky et al. 2011; Bellard et al. 2012; Kolbert, 2014; Ceballos et al. 2015). The spatial dynamics of speciation shape the structure of the modern latitudinal biodiversity gradient (LBG), where species richness increases away from the poles, peaking within the lower latitudes (Fenton et al. 2016a). Within this system, it has been proposed that the tropics act as both a ‘cradle’ and a ‘museum’, operating as the source of species originations, and also exhibit lower extinction rates, preserving global biodiversity (Jablonski et al. 2006, 2013). A number of recent studies, however, have begun to challenge the stability of this pattern through deep time, where evidence now suggests that speciation cradles may have operated at higher latitudes during intervals associated with heightened global temperatures (Archibald et al. 2010; Mannion et al. 2012; Mannion et al. 2014; Raja & Kiessling, 2021).

The nature of macroevolutionary processes within the marine realm are fundamentally distinct from their terrestrial counterparts, due to the relative lack of physical dispersal barriers that facilitate speciation through reproductive isolation (Mayr, 1942; Norris, 1999; 2000; Norris & Hull, 2012). Furthermore, the modern oceanic realm is comparatively understudied (Spalding et al. 2008; Cox et al. 2016) making predictions on the response of marine organisms to rapid climate change even more challenging.

The Cenozoic marine planktonic microfossil record represents an excellent biological archive to study spatially resolved macroevolutionary dynamics due to their generally cosmopolitan species distributions, high preservation potential, and abundance in marine sediments. In particular, the macroperforate planktonic foraminifera, a group of globally distributed single-celled marine protists with a phylogenetic history spanning back to the Early

Jurassic (Lowery et al. 2020), exhibit the most complete species-level fossil record for any Cenozoic fossil group (Aze et al. 2011; Fordham et al. 2018). Moreover, their macroevolutionary history is intrinsically linked to the secular and transient climate trends that typify much of the Cenozoic geological record, which has led to their widespread use in addressing fundamental questions on evolution and palaeoceanography through geological time (e.g., Pearson et al. 2001; Schmidt et al. 2004; Liow et al. 2010; Ezard et al. 2011; Hönisch et al. 2012; Peters et al. 2013; Tucker et al. 2019; Lowery & Fraass, 2019; Lowery et al. 2020; Boscolo-Galazzo et al. 2021).

The utility of the planktonic foraminifera has been enhanced by the production of several micropalaeontological occurrence datasets (Lazarus, 1994; Spencer-Cervato, 1999; Diepenbroek et al. 2002; Siccha & Kučera, 2017; Renaudie et al. 2020). The most recent effort, the Triton dataset (Fenton & Woodhouse et al. 2021), which has compiled all Cenozoic planktonic foraminiferal occurrence datasets including many new records, represents the largest group-specific fossil occurrence dataset ever created with 512,922 individual specimen occurrences, permitting the inspection of biogeographic patterns within the planktonic foraminiferal record at a greater resolution than ever before.

Here, the unparalleled phylogeny and biogeographic record of the Cenozoic planktonic foraminifera is used to examine and assess the relationship between Cenozoic environmental records (the ratios of carbon $\delta^{13}C$ and oxygen $\delta^{18}O$ stable isotopes, (Westerhold et al. 2020), benthic marine temperature (Cramer et al. 2011), and atmospheric CO_2 (Foster et al. 2017; Rae et al. 2021)) and the spatial dynamics of speciation and extinction palaeolatitudes. The effects of the “Greenhouse” and “Icehouse” climate regimes are explored (e.g., Westerhold et al. 2020), as well as species-specific ecological habits on spatio-temporal patterns of speciation and extinction. Triton (Fenton & Woodhouse et al. 2021) is used to test 1) whether speciation is more likely in some geographic regions, and whether this is affected by the climate regime; 2) whether sampling efforts and carbonate preservation affects the spatial patterns observed within speciation and extinction; 3) whether species become extinct proximally or distally from their palaeolatitude of speciation; and 4) whether species are found within their palaeolatitude of speciation throughout their entire stratigraphic range.

4.2 Methods

The Triton dataset (Fenton & Woodhouse et al. 2021) was downloaded, and the 337 Cenozoic macroperforate planktonic foraminiferal species recognised in Lamyman et al. (in prep) were assigned to their chronostratigraphically-determined speciation and extinction datums in accordance with Aze et al. (2011) & Lamyman et al. (in. prep). All occurrences located outside of species assigned stratigraphic ranges were removed to eliminate occurrence data likely caused by recent taxonomic revisions, misidentification, and/or reworking which may create artificial “tails” in speciation and extinction records (Liow et al. 2010). In total, 115,420 individual occurrences and 9 species were removed, leaving 328 species present in the dataset. Of the remaining species, 326 speciate and 284 become extinct during the Cenozoic (the difference being the 32 extant taxa, and two muricohedbergellids which speciated in the Late Cretaceous (Aze et al. 2011; Lowery & Fraass, 2019; Lamyman et al. in prep.).

4.2.1 Climatic drivers in palaeolatitude of speciation

To assess whether species-specific ecological habits and the global environmental conditions at the time of speciation have an impact on the palaeolatitude of speciation within Cenozoic macroperforate planktonic foraminifera, the earliest/oldest dated occurrence of all species within their assigned stratigraphic ranges (Aze et al. 2011; Lamyman et al. in prep.) was calculated, and the palaeolatitudinal data extracted. Additionally, all sample ages in Triton were rounded to one decimal place (100 kyr resolution) to allow for minor flexibility in the ages of samples calculated from Triton (Fenton & Woodhouse et al. 2021), and where species have more than one earliest/oldest rounded age occurrence in Triton, the mean and median of these age occurrences were calculated to account for the difficulties which can arise when trying to accurately assign first and last fossil occurrences (Jaanusson, 1976; Signor & Lipps, 1982; Marshall et al. 1998).

I then extracted the Cenozoic abiotic parameters: benthic foraminiferal marine stable isotope ratios $\delta^{13}C$ (‰) and $\delta^{18}O$ (‰) (Westerhold et al. 2020), benthic foraminiferal marine temperature (°C) (Cramer et al. 2011), and atmospheric CO_2 (ppm) (Foster et al. 2017; Rae et al. 2021) from the specified literature, temporally binned the data to 88 intervals of equal length (0.75 Myr) and calculated the mean value of each parameter per bin (Table S1). All Cenozoic planktonic foraminiferal speciation occurrences from 66-33.9 Ma were assigned to the Greenhouse climate regime, and those from 33.9-0 Ma to the Icehouse to assess whether the underlying climate regime has an effect on the palaeolatitude of speciation. Species were also allocated to the specified "ecogroups" of Aze et al. (2011) to determine whether the palaeolatitude of speciation is affected by species-specific ecological habits. Species with no available ecological data (12 in total) were removed from the analysis. Finally, the quantity of Triton (Fenton & Woodhouse et al. 2021) samples located within the tropics (palaeolatitudes < 23.5 ° north or south of the equator), and extratropics (palaeolatitudes > 23.5 ° north or south of the equator) were measured. This position was defined as the area bounded by the current positions of the tropics of Cancer and Capricorn; however, it is acknowledged that an ecological and/or thermal assignment of the tropics defined on modern tropical conditions would be highly dynamic through geological time (Zhang et al. 2019; Crame, 2020; Raja & Kiessling, 2021). The proportion (%) of tropical samples per time bin was then calculated to determine whether latitudinal sampling intensity biases palaeolatitudinal speciation. This was an essential step as much of the early Cenozoic has a comparative scarcity of lower latitude samples in microfossil occurrence datasets (Table S1) (Renaudie et al. 2020; Fenton & Woodhouse et al. 2021).

The abiotic and sampling parameters (Table S1) were used to predict palaeolatitudes of speciation using generalized least squares (GLS) models fitted in R (R Core Team, 2021) using the package 'nlme' (Pinheiro et al. 2020). Models showed some evidence of temporal autocorrelation, but no evidence for heterogeneity in the residuals of the explanatory variables. The best fitting models (Tables 1-4) were evaluated using the Akaike Information Criterion (AIC). Model fitting was achieved by systematically dropping each explanatory variable and comparing model AIC values to determine whether the dropped term improved model performance (Zuur et al. 2009). The best fitting models ultimately required no autocorrelation functions (Tables 1-4).

4.2.2 Palaeolatitudinal dynamics from speciation to extinction

To test whether the palaeolatitude of speciation effects the ultimate palaeolatitude of extinction within the Cenozoic planktonic foraminifera, the previously calculated species-specific palaeolatitudes of earliest/oldest occurrences were paired with the latest/youngest occurrences for all 284 extinct species. Once again, where species had more than one latest/youngest occurrence when rounded to one decimal place (100 kyrs), the mean of these occurrences was calculated and compared with the mean palaeolatitude of speciation. Shapiro-Wilk tests were applied to determine whether speciation and extinction latitudes within the two different climate regimes are statistically significantly different from a normal distribution.

Finally, to investigate whether species maintain a presence within their palaeolatitude of speciation throughout their entire stratigraphic range, all species data were binned to 88 intervals of equal length (0.75 Myrs) spanning the entire Cenozoic. Species-specific palaeolatitudinal “ancestral ranges” were defined as the palaeolatitudinal band +/- 5° N & S of the mean palaeolatitude of speciation. Each time bin within this palaeolatitudinal band was then inspected for occurrences of each species and the total proportion (%) of occupied time bins calculated to determine how many species exhibit “ancestral range maintenance”; that is, species consistently document occurrences proximal (+/- 5° N & S) to their mean palaeolatitude of speciation throughout their entire stratigraphic range.

4.3 Results

4.3.1 Climatic drivers in palaeolatitude of speciation

GLS model fitting shows that a combination of the parameters *$\delta^{13}C$, temperature, proportion of tropical sampling* and *ecogroup* provide the best models for predicting the mean and median palaeolatitudes of speciation (Tables 1-2), where lower $\delta^{13}C$ values, higher *temperature,* and a lower *proportion of tropical sampling* are statistically significant and correlated with higher mean and median palaeolatitudes of speciation (Figure 1). The best model for predicting the earliest/oldest palaeolatitude of occurrence included the same parameters for predicting both the mean and median palaeolatitudes of speciation, however only *temperature* and the *proportion of tropical sampling* are statistically significant for predicting the earliest occurrence, where higher *temperature,* and a lower *proportion of tropical sampling* are correlated with higher earliest/oldest palaeolatitudes of occurrence (Tables 3A & 3B).

4.3.2 Palaeolatitudinal dynamics from speciation to extinction

The palaeolatitude of extinction in 70.8% of all species is > 5° away from their palaeolatitude of speciation (Table 4; Figure 2), and species that originated within the Greenhouse regime generally show a greater difference in their mean palaeolatitude of speciation and extinction (Table 4; Figure 2). Moreover, 38.2% of all Cenozoic species became extinct in the hemisphere opposite to where they speciated (40.6% and 35.8% of Icehouse and Greenhouse species, respectively). Shapiro-Wilk test results confirm that speciation and extinction palaeolatitudes are not normally distributed, displaying differentially multimodal skews towards the northern hemisphere across both climate systems (Figure 3). Of the 284 extinct Cenozoic taxa analysed in this study, only 32.7% of them exhibit constant “ancestral range maintenance”, where the ancestral palaeolatitudinal habitat of speciation (+/-

5° from the mean palaeolatitude of speciation) remained occupied for the entirety of the species range.

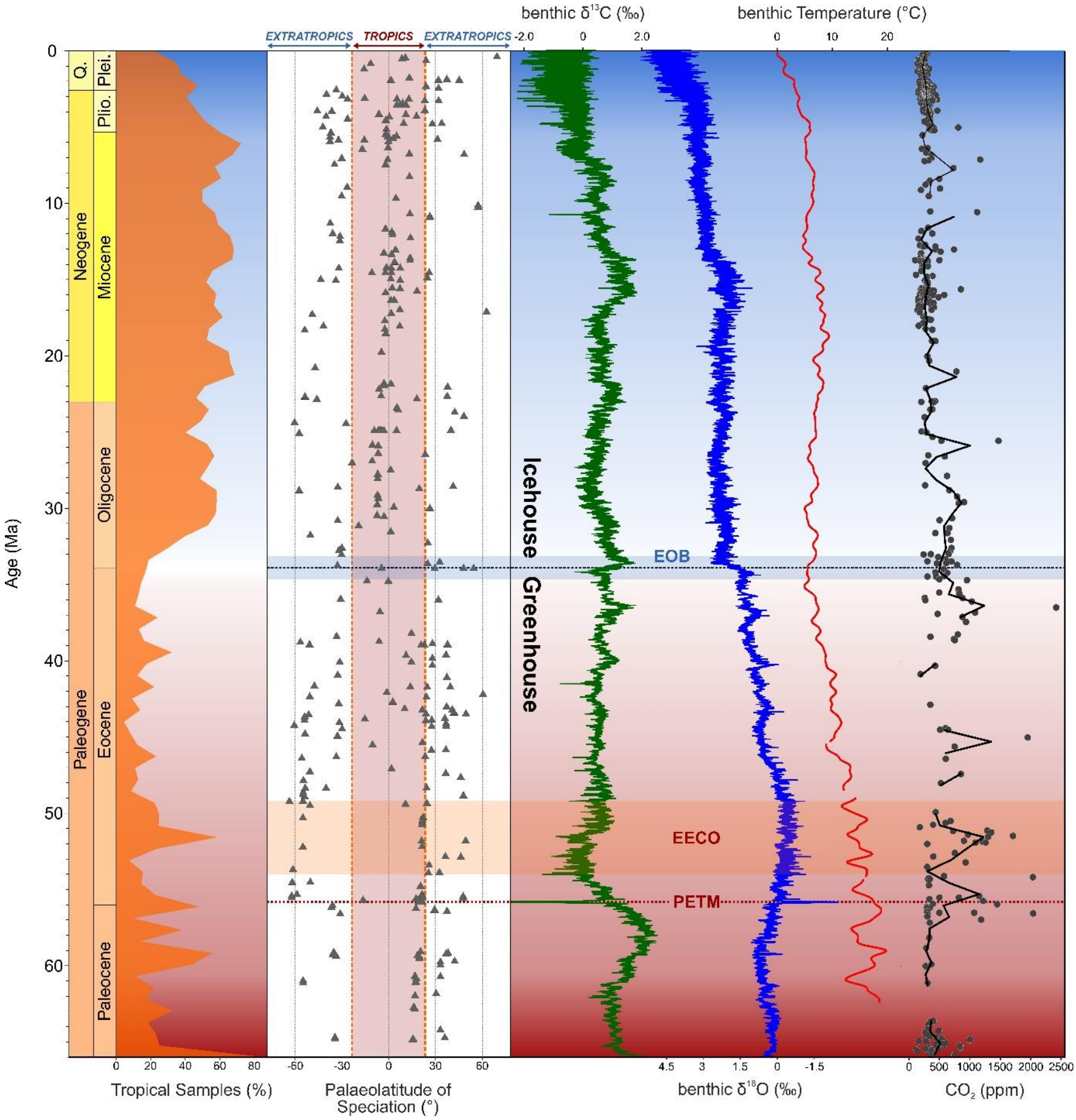

Figure 1. Cenozoic compilation of tropical sampling proportion (%), palaeolatitudinal location of all planktonic foraminiferal earliest occurrences with tropical/extratropical boundaries highlighted, Cenozoic abiotic climate parameters, and important climatic events. δ^{13}C and δ^{18}O from Westerhold et al. (2020), benthic (Mg/Ca) temperature from Cramer et al. (2011), atmospheric CO$_2$ data from Foster et al. (2017) and Rae et al. 2021), circles are individual data, bold line is mean value. PETM = Paleocene-Eocene Thermal Maximum, EECO = Early Eocene Climatic Optimum, EOB – Eocene-Oligocene Boundary.

Model	Parameters	AIC
Full model for mean palaeolatitude of speciation	$\delta^{13}C$, $\delta^{18}O$, CO_2, Temperature, Regime, Tropical sampling, Ecogroup	2462.126
Best model for mean palaeolatitude of speciation	$\delta^{13}C$, Temperature, Tropical sampling, Ecogroup	2456.422

Table 1A. Summary of GLS multiple regression analysis showing the full and best models for predicting the mean palaeolatitude of speciation.

Response	Parameters	Value	SE	t	*p*
Mean palaeolatitude of speciation	$\delta^{13}C$	-4.647403	1.849442	-2.512868	***0.0125***
	Temperature	1.252866	0.258683	4.843241	***< 0.0001***
	Tropical sampling	-0.201806	0.050738	-3.977405	***0.0001***
	Ecogroup2	2.668565	2.856974	0.934053	0.3510
	Ecogroup3	1.918832	2.271748	0.844650	0.3990
	Ecogroup4	3.679243	2.537226	1.450105	0.1481
	Ecogroup5	4.315506	7.436958	0.580278	0.5622
	Ecogroup6	-1.650017	7.470716	-0.220865	0.8254

Table 1B. Summary of best fitting GLS multiple regression model for predicting the mean palaeolatitude of speciation. Bold and italicized p-values values are statistically significant ($p < 0.05$).

Model	Parameters	AIC
Full model for median palaeolatitude of speciation	$\delta^{13}C$, $\delta^{18}O$, CO_2, Temperature, Regime, Tropical sampling, Ecogroup	2481.623
Best model for median palaeolatitude of speciation	$\delta^{13}C$, Temperature, Tropical sampling, Ecogroup	2475.778

Table 2A. Summary of GLS multiple regression analysis showing the full and best models for predicting the median palaeolatitude of speciation.

Response	Parameters	Value	SE	t	*p*
Median palaeolatitude of speciation	$\delta^{13}C$	-5.081840	1.911764	-2.658193	***0.0083***
	Temperature	1.333718	0.267401	4.987714	***< 0.0001***
	Tropical sampling	-0.212330	0.052448	-4.048399	***0.0001***
	Ecogroup2	2.949429	2.953249	0.998706	0.3188
	Ecogroup3	1.888602	2.348302	0.804241	0.4219
	Ecogroup4	4.627803	2.622726	1.764501	0.0787
	Ecogroup5	4.258743	7.687571	0.553978	0.5800
	Ecogroup6	-1.467121	7.722467	-0.189981	0.8495

Table 2B. Summary of best fitting GLS multiple regression model for predicting the median palaeolatitude of speciation. Bold and italicized p-values values are statistically significant ($p < 0.05$).

Model	Parameters	AIC
Full model for earliest/oldest palaeolatitude of speciation	$\delta^{13}C$, $\delta^{18}O$, CO_2, Temperature, Regime, Ecogroup, Tropical sampling	2814.231
Best model for earliest/oldest palaeolatitude of speciation	$\delta^{13}C$, Temperature, Tropical sampling, Ecogroup	2808.989

Table 3A. Summary of GLS multiple regression analysis showing the full and best models for predicting the earliest/oldest palaeolatitude of speciation.

Response	Parameters	Value	SE	t	*p*
Earliest/oldest palaeolatitude of speciation	$\delta^{13}C$	-3.210951	1.888611	-1.700166	0.0900
	Temperature	1.194357	0.271266	4.402904	***< 0.0001***
	Tropical sampling	-0.209995	0.053725	-3.908729	***0.0001***
	Ecogroup2	2.476936	2.931761	0.844863	0.3988
	Ecogroup3	-0.323397	2.364913	-0.136748	0.8913
	Ecogroup4	4.764311	2.653047	1.795788	0.0734
	Ecogroup5	1.449767	8.101402	0.178953	0.8581
	Ecogroup6	-1.634005	8.131168	-0.200956	0.8409

Table 3B. Summary of best fitting GLS multiple regression model for predicting the earliest/oldest palaeolatitude of speciation. Bold and italicized p-values values are statistically significant ($p < 0.05$).

4.4 Discussion

4.4.1 Cenozoic drivers of speciation palaeolatitudes

Regardless of whether the mean, median, or earliest/oldest palaeolatitude of speciation is assessed through GLS modelling, both *temperature* and the *proportion of tropical sampling* are significant parameters for predicting the distance from the equator (Tables 1-3). The presence of a consistent, positive relationship with *temperature*, despite the clear bias against early Cenozoic tropical speciation due to the inherently lower *proportion of tropical sampling* (Renaudie et al. 2020; Fenton & Woodhouse et al. 2021) is evidence that *temperature* is the primary abiotic driver of higher palaeolatitudes of speciation for Cenozoic macroperforate planktonic foraminifera (Figures 1-4). This extratropical speciation (Raja & Kiessling, 2021) is likely facilitated by thermally restrictive tropical temperatures limiting low-latitude habitability (Huber, 2008; Tewksbury et al. 2008; Bown & Pearson, 2009; Speijer et al. 2012; Aze et al. 2014; Frieling et al. 2017, 2018; Asseng et al. 2021).

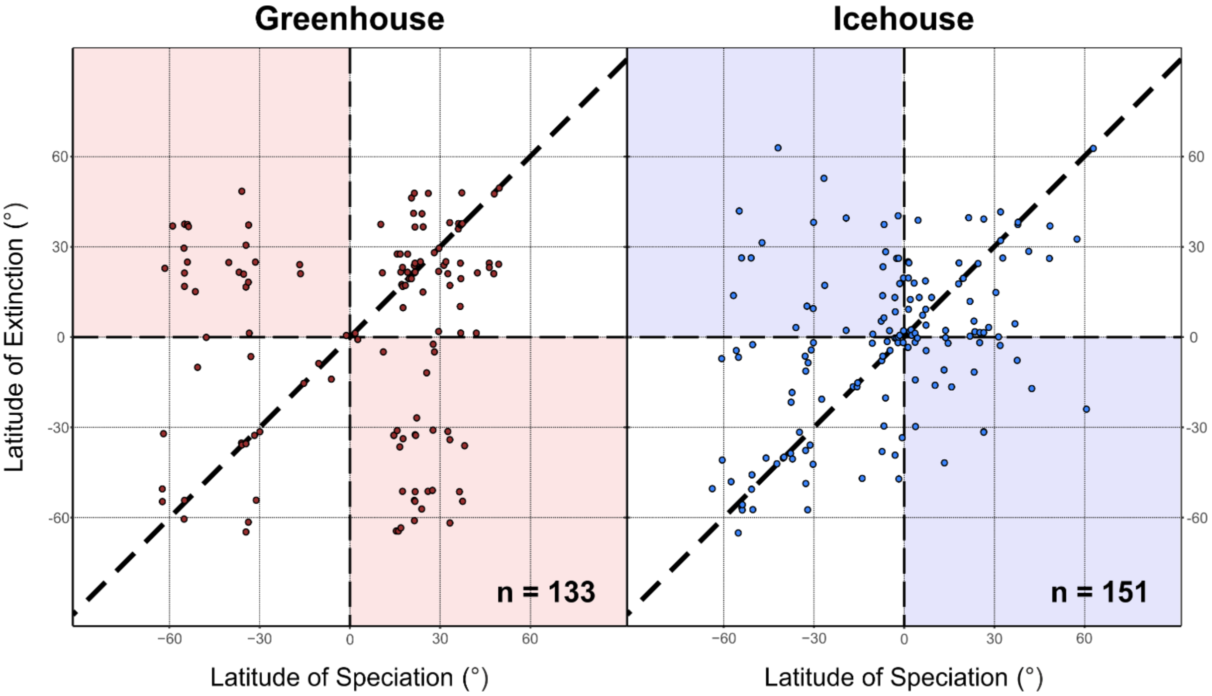

Figure 2. Comparison between the mean palaeolatitude of speciation and extinction within Greenhouse and Icehouse regimes. Points located along the dashed line indicate species with similar speciation and extinction palaeolatitudes. Points located above the bold dashed line are species that have last occurrences located north of their speciation palaeolatitude, and points below line have last occurrences located south of their speciation palaeolatitude. Points located within the coloured shaded areas indicate species that have switched hemisphere between their speciation and extinction palaeolatitudes.

The most likely cause of the negative relationship observed between the mean and median palaeolatitude of speciation with $\delta^{13}C$ (Tables 1-2) is the pronounced stable carbon isotope volatility associated with the early Cenozoic Greenhouse regime hyperthermals (Figure 1) (Westerhold et al. 2020). Here, the release of substantial quantities of isotopically light volcanogenic carbon associated with the phased eruptions of the North Atlantic Igneous Province increased global *temperature* whilst reducing global marine $\delta^{13}C$ ratios (Figure 1) (Gutjahr et al. 2017; Jones et al. 2019a; Hayes & Hönisch, 2020; Westerhold et al. 2020).

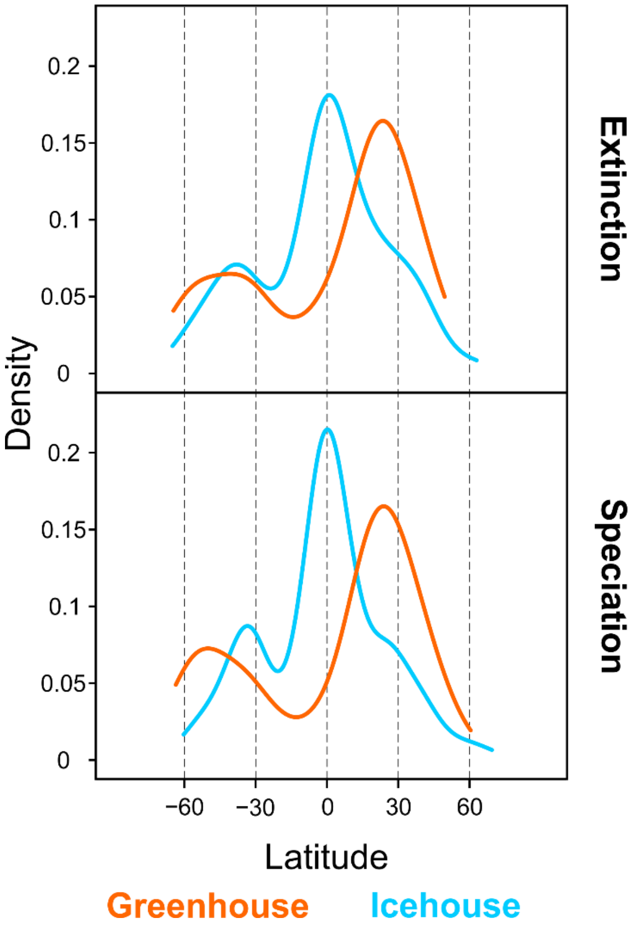

Figure 3. Kernel density estimates of the earliest (Speciation) and latest (Extinction) palaeolatitudes of species occurrences. Shown are the probability density functions for the Greenhouse and Icehouse taxa.

4.4.2 Palaeolatitudinal dynamics in speciation cradles

Of the 326 Cenozoic study taxa which speciated, and 284 which became extinct in this study, 35.0% and 58.6% respectively exhibit a tropical speciation palaeolatitude in the Greenhouse and Icehouse regimes, (Figures 1-4; Table 1), where the tropics are defined as the regions ± 23.5° north and south of the equator through the entire Cenozoic record. These data support recent work by Raja & Kiessling (2021) highlighting the presence of extratropical cradles through much of the early Cenozoic. However, in contrast with the results of their study, data here suggest that species from the Icehouse exhibit a tropical cradle in accordance with the “out of the tropics” (OTT) hypothesis of Jablonski et al. (2006, 2013) as opposed to one showing equivalent or random tropical/extratropical speciation (Table 1) (Raja & Kiessling, 2021). Within both this study, and that of Raja & Kiessling (2021) however, Greenhouse regime speciation patterns contrast with the OTT hypothesis, within which the tropics generate the majority of species ancestral stock.

	Cenozoic	Greenhouse	Icehouse
Mean speciation latitude	0.41°	2.40°	-1.54°
Mean extinction latitude	-0.05°	1.97°	-1.81°
Mean diff. speciation + extinction	26.4°	32.3°	21.1°
Tropical “Cradle”	47.2% (57.0%)	35.0% (47.0%)	58.6% (69.1%)
Extratropical “Cradle”	52.8% (43.0%)	65.0% (53.0%)	41.4% (30.9%)
Tropical “Grave”	48.9% (59.7%)	39.0% (52.7%)	57.5% (65.9%)
Extratropical “Grave”	51.1% (40.3%)	61.0% (47.3%)	42.5% (34.1%)
Hemisphere switch	38.2%	40.6%	35.8%

Table 4. Mean palaeolatitudes of speciation and extinction, mean difference in the palaeolatitudes of speciation and extinction location, proportion of taxa which speciate and become extinct in the tropics (23.5° north and south of the equator) and extratropics (values in brackets use a tropical/extratropical boundary of 30° north and south of the equator as assigned in Raja & Kiessling (2021)), and proportion of species which become extinct in the hemisphere opposite to their speciation.

Following the Paleocene-Eocene Thermal Maximum (PETM, ~56 Ma), speciation palaeolatitudes of the planktonic foraminifera exhibit sustained poleward migration (Figures 1 & 4) before shifting back towards the equator after the Early Eocene Climatic Optimum (EECO), the peak of Cenozoic warming (Inglis et al. 2020). Furthermore, the predominantly northern skew seen within the palaeolatitudes of speciation and extinction data (Figure 3) is a typical feature of Cenozoic fossil occurrence datasets, where historically, palaeontological sampling efforts have been concentrated within the northern hemisphere trans-Atlantic region (e.g., Vilhena & Smith, 2013; Menegotto & Rangel, 2018), however, there is notably greater variability observed within the Icehouse regime (Figures 1-4) which may be associated with the global cooling that accompanied the onset of the Eocene-Oligocene Boundary (EOB, ~33.9 Ma) (Figure 1). The long-term Cenozoic expansion of continental-scale ice sheets aided the development of steeper vertical and latitudinal temperature gradients through the intensified upwelling of cool, nutrient-rich bottom waters (Schmidt et al. 2004; Coxall et al. 2005; Edgar et al. 2007; Liu et al. 2009; Pälike et al. 2012; Villa et al. 2014; Jones et al. 2019b; Sarkar et al. 2019; Zhang et al. 2019; Hutchinson et al. 2021). This, in turn, steepened temperature gradients and exacerbated planktonic foraminiferal niche partitioning within the global ocean structure (Schmidt et al. 2004; Al-Sabouni et al. 2007; Boscolo-Galazzo et al. 2021). Improved post-Greenhouse habitability of the cooler tropics likely enhanced low-latitude speciation (Figures 1-4), and the substantial changes in palaeoceanographic gradients may have contributed to greater ecological stability within the mid-latitudinal subtropical gyres (Fenton et al. 2016; Schiebel & Hemleben, 2017) which are the likely locales of Icehouse extratropical cradles (Figures 1-4).

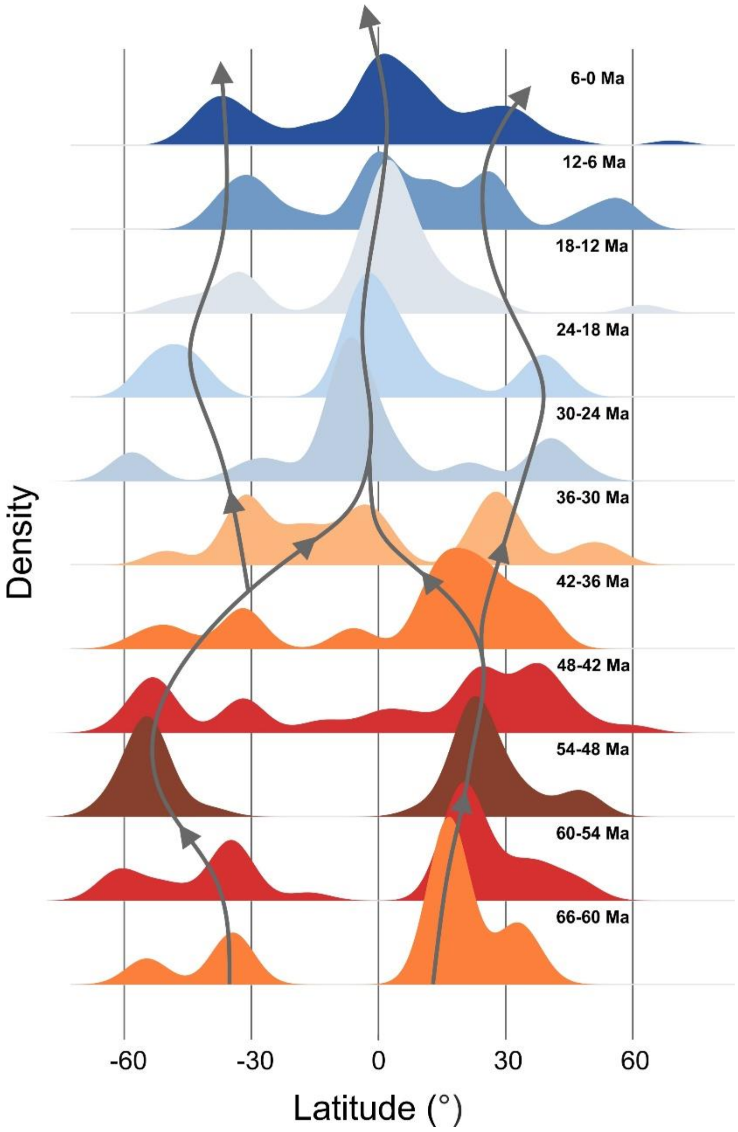

Figure 4. Kernel density estimates of Cenozoic planktonic foraminiferal speciation palaeolatitudes through time. Shown are the probability density functions for all species earliest/oldest (speciation) appearance in Triton assigned to 6 Myr time bins. Schematic arrows indicate the approximate evolution of speciation locales through time. Colour scheme derived from Westerhold et al. (2020) to indicate relative global temperatures during time bins.

The significantly more heterogenous structure of the Icehouse Ocean, coupled with the stepwise obstruction of tropical/subtropical waters caused by the gradual closure of the Tethyan and Central American Seaways (Crame & Rosen, 2002; Brierly & Fedorov, 2010;

Hamon et al. 2013; Matthews et al. 2016), may have contributed to the notable rise in diversity which approaches the Recent (Aze et al. 2011; Ezard et al. 2011; Peters et al. 2013; Fraass et al. 2015; Lowery et al. 2020). Low latitude dispersal barriers have likely also increased biogeographic marine habitat partitioning, fostering some of the notable and potential examples of endemism within Neogene planktonic foraminifera (Scott et al. 1990; Rögl 1999; Norris, 1999, 2000; Crundwell, 2018; Spezzaferri et al. 2018a; Lam & Leckie, 2020; Kiss et al. in review). An intensified Icehouse climate may have also played a crucial role in shaping the diversity observed within modern planktonic foraminiferal cryptic genotypes (Darling & Wade, 2008; Aurahs et al. 2009; Morard et al. 2009, 2013, 2019; Ujiié et al. 2010; Norris & Hull, 2012; Weiner et al. 2012; 2014; André et al. 2014; Ujiié & Ishitani, 2016), though further work is required on the quantification of planktonic foraminiferal cryptic diversity within deep time (André et al. 2013). However, if fossil cryptic species are comparatively lacking to the modern ocean, their absence may further reinforce the legitimacy of the biological nature of the observed increase in diversity towards the Recent (Uhen & Pyenson, 2007; Jablonski et al. 2003; Sahney & Benton, 2017; Valenzuela-Toro & Pyenson, 2019; Pimiento & Benton, 2020).

Both GLS model results, and the lack of speciation in the lower palaeolatitudes of the early Cenozoic (Table 4; Figures 1-4) reinforces the existence of extratropical cradles (Archibald et al. 2010; Mannion et al. 2012; Mannion et al. 2014; Raja & Kiessling, 2021). However, despite the likelihood that thermally prohibitive equatorial temperatures restrict tropical speciation and biodiversity throughout Greenhouse regimes (Huber, 2008; Tewksbury et al. 2008; Bown & Pearson, 2009; Mannion et al. 2012; Speijer et al. 2012; Sun et al. 2012; Aze et al. 2014; Frieling et al. 2017, 2018; Allen et al. 2020; Asseng et al. 2021), the proportion of species which become extinct in the hemisphere opposite to their hemisphere of speciation is greatest during the Greenhouse (Table 4; Figure 2). This may provide further support to previous inferences that environments/climates inherently subject to greater environmental variability may produce more ecologically resistant taxa (Liow et al. 2010; Chapter 3, herein). Planktonic foraminiferal species evolving within the Greenhouse regime that speciated at the higher extratropical palaeolatitudes would be inherently subjected to greater seasonality (Lutz et al. 2008; Zhang et al. 2019), and therefore potentially more ecologically capable to successfully traverse the tropics and establish a population in the opposing hemisphere (Figure 2).

4.4.3 Speciation dynamics and the Cenozoic sedimentological record

The carbonate saturation state of the ocean must also be considered in deep-time analyses of the calcareous microfossil record, as marine carbonate preservation is ultimately controlled by the interactions between sources and sinks of the carbon cycle which regulate atmospheric CO_2 (Pälike et al. 2012; Greene et al. 2019; Wade et al. 2020; Dutkiewicz & Müller 2021; Komar & Zeebe, 2021). The Eocene-Oligocene Boundary (EOB) (33.9 Ma) was typified by a significant deepening of the global carbonate compensation depth (CCD) following the onset of permanent Antarctic glaciation (Coxall et al. 2005; Edgar et al. 2007; Liu et al. 2009; Pälike et al. 2012; Villa et al. 2013; Sarkar et al. 2019; Hutchinson et al. 2021), resulting in enhanced rates of carbonate preservation and biogenic carbonate burial in the equatorial Pacific (Norris, 2000; Schmidt et al. 2006; Pälike et al. 2012; Wade et al. 2020; Dutkiewicz & Müller 2021). This would no doubt lead to an increased occurrence of preserved planktonic foraminifera within the lower latitudes (Figures 1-4), changing the palaeolatitudinal representation of speciation cradles which are likely partially influenced by physical constraints of early Cenozoic marine chemistry. The relative paucity of tropical records which characterizes the early Cenozoic of microfossil occurrence datasets (Renaudie et al. 2020; Fenton & Woodhouse, et al. 2021) has no doubt contributed to some aspects of the observed patterns in this study (Tables 1-4; Figures 1-4), however the transition from predominantly extratropical to tropical cradles through the Cenozoic is clearly linked with secular temperature trends in Cenozoic climate as evidenced by the model results (Tables 1-4). It is currently indeterminate how much of this pattern may be attributed to a lack of deep-sea low latitude samples, or just low-latitude carbonate preservation, however future targeted scientific ocean drilling of topographic features situated in the palaeotropics that have consistently remained above the CCD may better confirm the timing and extent of the initiation of Cenozoic tropical cradles.

4.4.4 Ancestral range maintenance

Only 32.7% of all Cenozoic planktonic foraminiferal species demonstrate “ancestral range maintenance”, this observation, and the substantial mean distances between speciation and extinction palaeolatitudes (Table 4) suggests that the majority of the group potentially exhibit pre-extinction biogeographic range contractions consistent with the “contagion hypothesis” of Channell & Lomolino (2000). Here, prior to extinction, species biogeographic range contracts away from selection pressures, which may be toward the periphery of the species range. This is in contrast to the “demographic hypothesis”, where biogeographic range contracts towards the core of the species habitat (Channell & Lomolino, 2000; Brombacher et al. 2021). A common factor amongst Cenozoic species which exhibit “ancestral range maintenance” appears to be a generally shorter stratigraphic range (Supplementary Data). As marine plankton species require multiple millions of years to establish significant populations through the world oceans (Liow & Stenseth, 2007; Liow et al. 2010), shorter ranged species, which are more limited to their ancestral range, may be more susceptible to the demographic hypothesis (Channell & Lomolino, 2000), at the analytical resolution of this study at least.

4.4.5 Climate development and planktonic foraminiferal speciation

The Cenozoic macroperforate planktonic foraminiferal fossil record is the most complete fossil record available to science (Aze et al. 2011), yet only 11 (3.3%) of Cenozoic species in this study exhibit more than one palaeolatitudinally isolated (> 5°) earliest/oldest occurrence (100-kyr resolution). The three-dimensional structure of the pelagic ecosystem generally lacks the presence of impassable dispersion barriers which typify the terrestrial realm and should promote conditions suitable for sympatric speciation (Lazarus et al. 1995; Pearson et al. 1997; Spencer-Cervato & Thierstein, 1997; Norris, 1999; Johannesson, 2009; Norris & Hull, 2012; Knappertbusch, 2016; Faria et al. 2021). However, these interpretations would appear to support speciation mechanisms facilitated by geographic isolation (Mayr, 1942) within the Cenozoic planktonic foraminifera (Lazarus, 1983; Motoyama, 1997; Wei & Kennett, 1988; Lazarus et al. 1995; Norris, 1999, 2000; Schneider & Kennett, 1999; Norris & Hull, 2012; Pearson & Ezard, 2014; Hull & Norris, 2009; Bicknell et al. 2018; Bendif et al. 2019; Woodhouse et al. 2021).

A sympatric speciation signal within the Cenozoic planktonic foraminifera is likely muted by not only the methodology of sample age calculation in Triton (Fenton & Woodhouse et al. 2021), but also the nature of the palaeontological bounds on the precise identification of morphological speciation and extinction (Jaanusson, 1976; Signor & Lipps, 1982; Marshall et al. 1998), however mutually operative tectonic, hydrographic, and bathymetric barriers undoubtedly act to successfully facilitate marine speciation through the reproductive isolation of pelagic populations (Norris, 1999; 2000; Norris & Hull, 2012; Peters et al. 2013).

4.5 Conclusions

Cenozoic biogeographical distribution records demonstrate that there are considerable differences in the spatiotemporal nature of marine speciation and extinction dependent upon the global climate conditions that marine biodiversity is operating within. Though the latitudinal distributions of samples within Triton have a clear effect upon the patterns seen within the data, the cooling trend inherent to the climatic evolution of the last 66 Myrs appears to have sequentially modified planktonic foraminifera speciation and extinction locales, where warmer global temperatures have promoted speciation within higher palaeolatitudes. Following speciation and outward propagation, most species exhibit pre-extinction biogeographic range contraction away from external selection pressures, not towards their palaeolatitudinal ancestral range.

These observations provide strong evidence for advancing our understanding of the underlying biotic and abiotic mechanisms which drive evolution and extinction in the largest ecosystem on Earth. The verification of extratropical speciation cradles during the

Greenhouse regime requires further investigation due to the current paucity of equatorial records, however, the evidence for thermally induced vacation of the tropics during Greenhouse climates increases the likelihood that a bimodal latitudinal biodiversity gradient was in place for the macroperforate planktonic foraminifera. As the modern world accelerates towards abiotic conditions coeval to those estimated for the Greenhouse world of the early Cenozoic, significant changes to modern and future marine population distributions and speciation locales may be expected with unpredictable effects upon ecosystem function.

5. Adaptive ecological niche migration does not negate extinction susceptibility

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Abstract

Extinction rates in the modern world are currently at their highest in 66 million years and are likely to increase with projections of future climate change. Our knowledge of modern-day extinction risk is largely limited to decadal-centennial terrestrial records, while data from the marine realm is typically applied to high-order (> 1 million year) timescales. At present, it is unclear whether fossil organisms with common ancestry and ecological niche exhibit consistent indicators of ecological stress prior to extinction. The marine microfossil record, specifically that of the planktonic foraminifera, allows for high-resolution analyses of large numbers of fossil individuals with incredibly well-established ecological and phylogenetic history. Here, analysis of the isochronous extinction of two members of the planktonic foraminiferal genus *Dentoglobigerina* shows disruptive selection differentially compounded by permanent ecological niche migration, “pre-extinction gigantism”, and photosymbiont bleaching prior to extinction. Despite shared ecological and phylogenetic affinity and timing of

extinction, the marked discrepancies observed within the pre-extinction phenotypic responses are species-specific. These behaviours may provide insights into the nature of evolution and extinction in the open ocean and can potentially assist in the recognition and understanding of marine extinction risk in response to global climate change.

5.1 Introduction

Current extinction rates are estimated to be at least eight times higher than the background Cenozoic (< 66 Ma) average[1] and understanding the impacts of rapid climate change on global biodiversity is of critical importance for creating a sustainable future (https://sdgs.un.org/goals). An increasing body of evidence suggests climate state variability is potentially more important than the direction of temperature change with respect to heightened extinction rates[2,3]. As such, we look to the Cenozoic marine sedimentary record, which allows us to assess the impacts of high variability in climate state on extinct biodiversity[4,5]. In this study, we focus on the planktonic foraminifera, single-celled marine protists with a global distribution and the most complete Cenozoic species-level fossil record[6]. Their calcareous skeletons, or tests, preserve not only their entire life history, but also a biogeochemical expression of the surrounding water column (e.g., [7]). These features allow for high-resolution species-specific quantification of physiological and ecological adaptation through periods of climate variability (e.g., [8-21]).

Our analysis investigates the response of the planktonic foraminiferal genus *Dentoglobigerina*, of which two species (*Dentoglobigerina altispira* and *Dentoglobigerina baroemoenensis*) undergo an isochronous extinction at ~3.04 Ma, during a period associated with increasing climate state variability[22,23]. Through high-resolution (~5 kyr) paired morphometric and geochemical analyses, we demonstrate that despite the two species occupying the same ecological niche space and sharing close phylogenetic affinity, they exhibit species-specific ecological and morphological responses prior to extinction[24].

Morphological data enables the assessment of the relationship between body size and shape parameters likely to record long- and short-term morphometric trends in response to global climate[14] (see Methods for designation of size and shape parameters). Single-specimen planktonic foraminiferal geochemical records allow us to place species within discrete

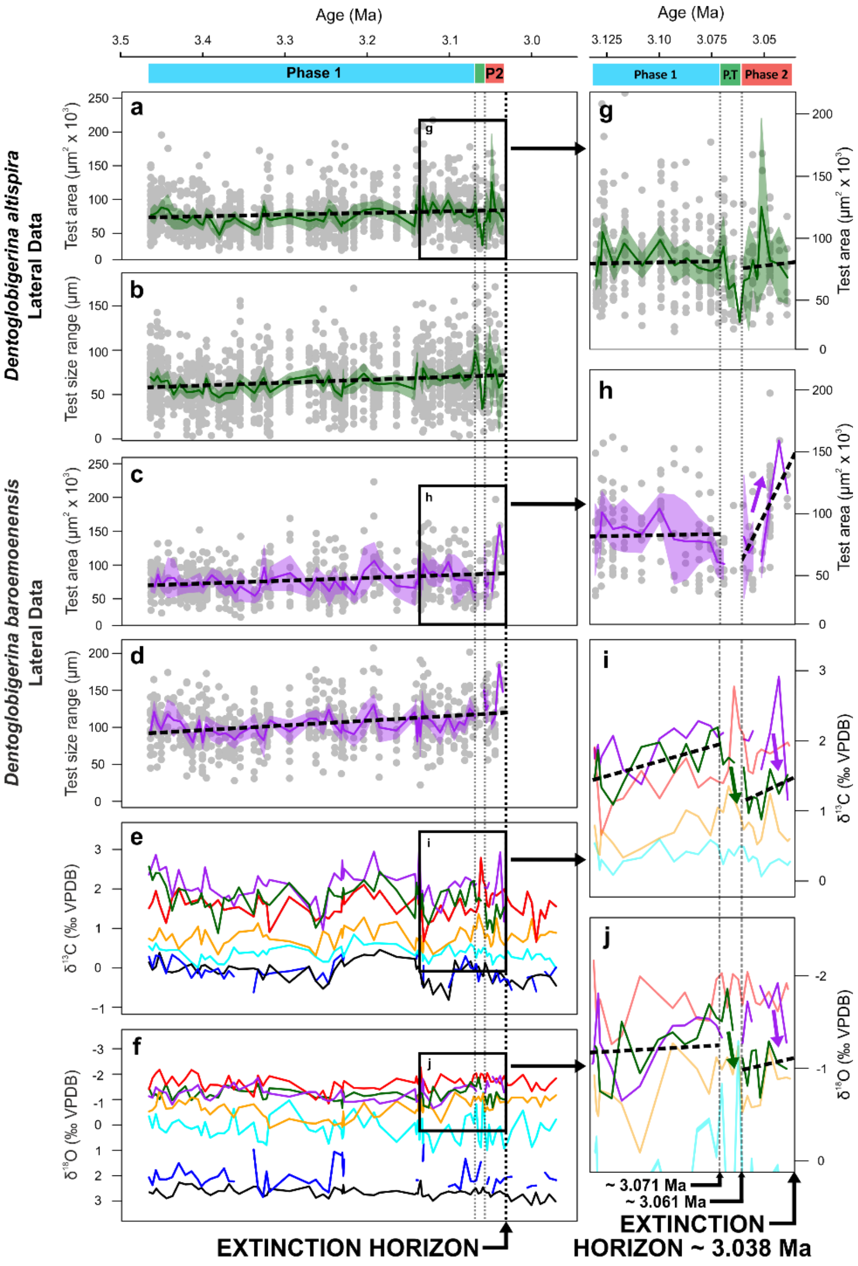

Figure 1. Stratigraphic log of Hole U1338A with geochemical and biotic records through dentoglobigerinid extinction event. a, *D. altispira* Area, b, and size range, c, *D. baroemoenensis* Area, d, and size range, e, Single and multi-specimens planktonic foraminiferal δ^{13}C, f, Single and multi-specimen planktonic foraminiferal δ^{18}O, g-j: blown up dentoglobigerinid Area, and isotope data in pre-extinction interval. Black = bottom-water*,* dark blue = subthermocline, cyan = thermocline, orange = subsurface*,* red = surface mixed layer, green = *D. altispira*, purple = *D. baroemoenensis.* Solid coloured lines for dentoglobigerinids are mean values of multiple single specimen analyses, shaded areas are 95% confidence intervals, black dashed lines are species trendlines, light vertical dotted lines indicate boundaries between "Phases", black vertical dotted line indicates extinction horizon.

ecological niches or “ecogroups” (see [6]), wherein the investigation of stable oxygen ($\delta^{18}O$) and carbon ($\delta^{13}C$) isotope ratios can be used to determine the relative degree of bathymetric and ecological separation within extant and extinct species[7,25].

The methods and hypotheses tested in this study highlight the utility of the marine micropaleontological record in assessing the pre-extinction ecological response of organisms at high-resolution during intervals of global climate variability.

5.2 Results

5.2.1 Morphological records

There is a long-term (~400 kyr) morphological trend approaching the dentoglobigerinid extinction interval (~3.038 Ma), where both species demonstrate a general increase in body size and range (Fig. 1). At ~3.071 Ma (Fig. 1), ~30 kyrs prior to the extinction of *D. altispira,* mean shape parameters indicate a deviation from relative morphological uniformity (Fig. S1), whereby the relationship between test area and aspect ratio (Fig. 2a) shows distinct changes due to a marked decrease in mean test area (Fig. 1a). This morphological excursion ends 10 kyrs later (3.061 Ma), where the size/shape values return to background values that were more typical prior to ~3.071 Ma (Figs. 1 & 2). We designate the respective sedimentary intervals preceding and succeeding these two morphological events to signify distinct ecological “Phases” in dentoglobigerinid pre-extinction response, herein termed “Phase 1” and “Phase 2”, respectively. Additionally, the 10 kyr interval encompassed by the two Phases is deemed to represent a “Phase Transition” (Fig. 1).

Within *D. baroemoenensis*, the size/shape relationship generally tends to show higher inter-sample variability than *D. altispira* throughout the record (Figs. 1 & 2). However, the most significant changes are seen following the Phase Transition, where there is marked increase in mean test size through the final ~10 kyrs prior to extinction (Figs. 1 & 2).

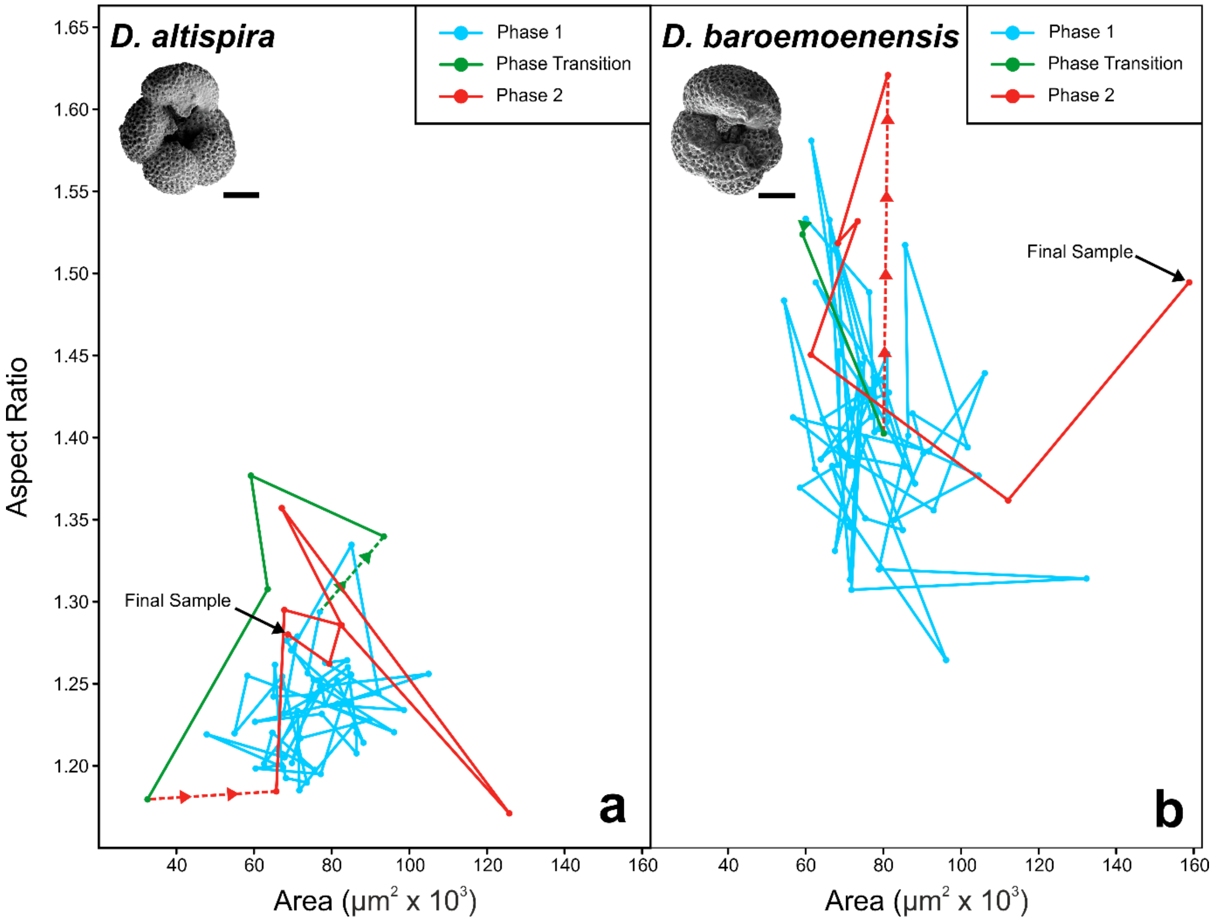

Figure 2. Sample means of lateral Area and Aspect Ratio of a, *D. altispira,* and b, *D. baroemoenensis*. Blue = Phase 1, green = Phase Transition, Red = Phase 2. Initiation of the Phase Transition is defined by the excursion in *D. altispira* morphometric data (see Morphological Records). Initiation of Phase 2 is defined *D. altispira* morphometric data returning to Phase 1 variability (see Morphological Records), and additionally by geochemical excursions in *D. altispira* stable isotope data (see Geochemical Records, Fig. 1). Scale bars = 100 μm.

5.2.2 Geochemical Records

Generally, dentoglobigerinid specimens exhibit stable isotope values typical of modern symbiont-hosting surface mixed-layer dwellers[25] (Fig. 3, SI), with high $\delta^{13}C$ and low $\delta^{18}O$, respectively. At ~3.061 Ma, contemporaneous with the initiation of Phase 2 (Figs. 1 & 2), *D. altispira* $\delta^{13}C$ and $\delta^{18}O$ signals exhibit significant, permanent negative and positive shifts, respectively, to values more consistent with species living in the subsurface, rather than the surface mixed-layer (Fig. 1i, j). This signal is not reflected by *D. baroemoenensis* at this time, and it is only in the final sample prior to extinction (~3.038 Ma) that a substantial negative $\delta^{13}C$, and positive $\delta^{18}O$ excursion consistent with the occupation of a deeper living-depth is seen in this species (Fig. 1i, j).

5.2.3 Statistical Analyses

Our data and linear models (see SI, Tables S1-4) identify trends in dentoglobigerinid morphology and ecology that support the designation of distinct ecological "Phases" in the final ~30 kyrs of our *Dentoglobigerina* species. Phase 1 is typified by stable morphological and geochemical background conditions from 3.466-3.071 Ma (Figs. 1 & 2). At this point the Phase Transition commences, identified by the morphological excursion of *D. altispira* (Figs. 1 & 2). Finally, 10 kyrs later Phase 2 initiates, marked by the coeval end of the period of diminished size in *D. altispira*, and the geochemical excursion representing a shift in its ecological niche (Figs. 1-3). For *D. baroemoenensis,* samples sourced from the Phase Transition are notably lacking in specimens, and enhanced size increase and morphological stochasticity is observed through much of Phase 2, (Figs. 1 & 2).

Models tested whether the abiotic conditions of the paleo-water column (signified by the stable isotopic signature of the present extant species with known living depths[6]), responded in or out of tandem with the dentoglobigerinid signature. Throughout Phase 1 the

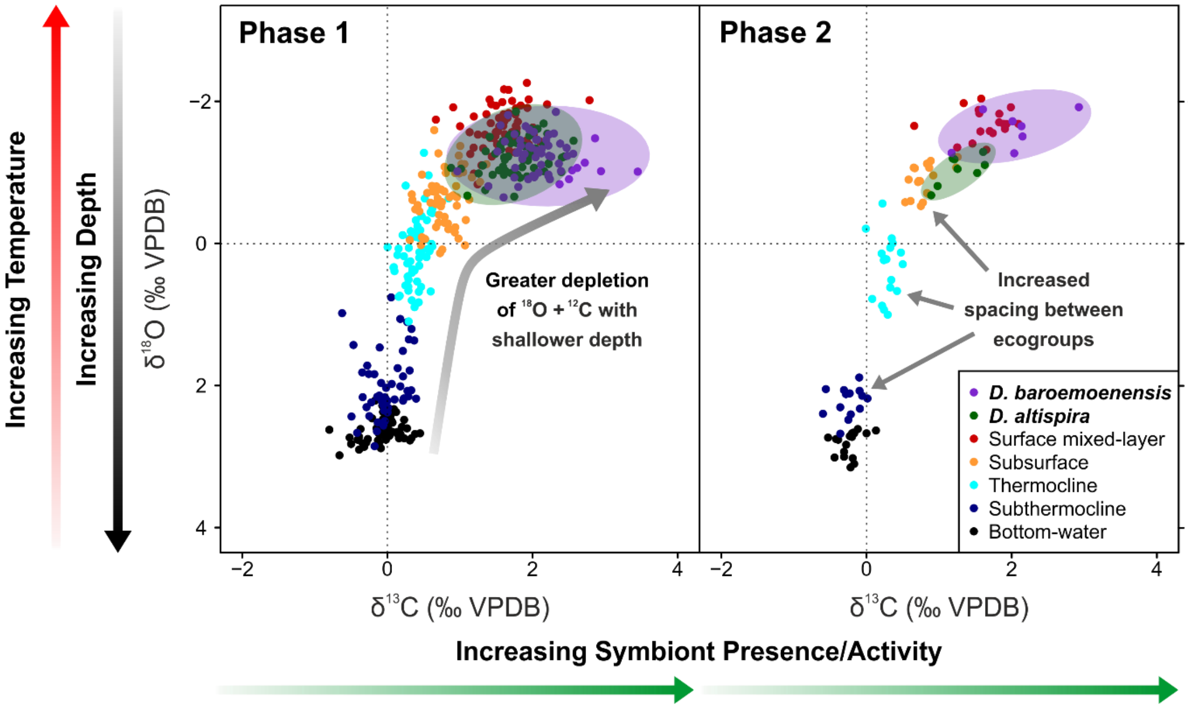

Figure 3. $\delta^{13}C$ and $\delta^{18}O$ cross-plots through Phase 1 and Phase 2. Black = Bottom-water, dark blue = subthermocline, cyan = thermocline, orange = subsurface, red = surface mixed layer, green = *D. altispira*, purple = *D. baroemoenensis. Dentoglobigerina* measurements are single specimens, others are multiple specimens.

dentoglobigerinids have isotopic signals that are consistent with a surface mixed-layer species which hosts photosymbiotic algae[6,25] (Figs. 1 & 3) and the two dentoglobigerinid species δ^{18}O signals respond in tandem (Tables S1 & S2). In Phase 2, there is a marked decoupling in the δ^{13}C signal of the two species (Tables S3 & S4) potentially indicating a disruption of photosymbiosis for *D. altispira,* but not for *D. baroemoenensis,* which maintains its ecological affinity up to the sample preceding extinction (Fig. 1i, j). Additional linear models testing the relationship between dentoglobigerinid morphology and environment show that as bottom water δ^{18}O becomes more positive and δ^{13}C more negative (e.g., as mean global temperature decreases/ice extent increases) dentoglobigerinid test area increases throughout Phase 1 (Tables S1 & S2). However, for *D. altispira*, this signal is lost in Phase 2, and for *D. baroemoenensis* the signal switches to increased test area mirroring more negative bottom-water δ^{18}O (Tables S3 & S4).

Grubbs' test[26] results (Table 1) indicate that outlier samples with statistical significance tend to be grouped within either the Phase Transition or Phase 2 for *D. altispira*, whereas all significant *D. baroemoenensis* outliers are represented by the final sample. Mann-Whitney U test[27] results (Table 2) show a significant difference between the *D. altispira* δ^{13}C signal of Phases 1 and 2. For *D. baroemoenensis*, Mann-Whitney U and z-test results (Table 2) indicate that the δ^{18}O signature, and the umbilical and lateral test area and size range records are significantly different between the two phases.

5.3 Discussion

The Cenozoic planktonic foraminiferal fossil record documents a strong positive correlation between test size and the degree of global marine latitudinal and vertical temperature gradients[22,28], however the largest intraspecific test sizes tend not to be analogous with species' ecological optima[29,30]. In Phase 1, dentoglobigerinid test size data shows a gradual relative increase through time (Figs. 1; S1) likely representing a response to the development of temperature gradients associated with the intensification of northern hemisphere icesheets[22,23]. At the initiation of the Phase Transition (~3.071 Ma) stepwise disruption in both morphology and geochemical signatures are likely indicative of disruptive selection and "bet-hedging"[31,32], a typical response to the propagation of terminal stress levels preceding extinction[33,34]. Previous studies[15,16] document increasing growth asymmetry and morphological trait variance as responses to abiotic forcing, wherein species produce offspring with high inter-individual phenotypic variability during unfavourable environmental conditions to improve mean population fitness[15,35-37].

In the case of *D. altispira*, the ecological end-result following the Phase Transition approaching the termination of the record appears to be permanent dwelling depth migration from a surface mixed layer habit down to one more equable to the subsurface (Figs. 1 & 3), supported by Mann-Whitney U test results (Table 2) on $\delta^{13}C$ signals between Phase 1 to 2 (Figs. 1 & 3). Significantly, *D. baroemoenensis* displays almost total absence during the Phase Transition (Fig. 1), supporting the prevalence of environmental conditions detrimental to dentoglobigerinid ecology. Upon its return, it shows a dramatic increase in lateral and umbilical area (Figs. 1; S1), where Mann-Whitney U test and z-test results indicate significantly different body size and range to Phase 1 (Table 2). These changes, which we term "pre-extinction gigantism", are antithetical to the "pre-extinction dwarfing"[10,38] previously documented in several other species, and may represent a response to the steepening of vertical and latitudinal water column temperature gradients associated with cryosphere development[22,23], typified by more distinct spacing between the geochemically assigned ecological habits during Phase 2 (Fig. 3).

The minor general trend of increasing body size range in both species (Fig. 1a, c) potentially infers long-term mitigation of external environmental pressures expressed through rising polymorphism. Further research is required; however, such behaviour may be characteristic of temporally long ranging species[39] when subjected to global climate state variations which deviate far from their ancestral ecosystem[40,41].

The study species share close phylogenetic and ecological affinity[39], maintain high-order morphological likeness from speciation, and undergo isochronous extinction, yet the phenotypic responses recorded prior to extinction are species-specific. Rapid within-clade character change, cladogenesis, and extinction during periods of detrimental environmental change are likely common-place within the history of life[33], and phylogenetically and ecologically adjacent taxa can exhibit similarities in selection pressures which do not necessarily trigger an adaptive response in the same direction[33,40].

For *D. altispira*, migration from the surface mixed layer to the subsurface may be compounded either by a photosymbiont reduction/suppression[18], or adoption of a facultative symbiotic ecological strategy, recognized to enhance flexibility of nutritional sources through minimal energetic investment[42,43]. This proposed adaptation is suggested over total algal photosymbiont "bleaching"[9,11,18,21,44], as *D. altispira* continues to present $\delta^{13}C$ enrichment higher than values observed in the asymbiotic, subsurface-dwelling taxa analysed in this study[43], yet similar $\delta^{18}O$ values (Figs. 1 & 3).

For *D. baroemoenensis*, water column temperature gradient dynamics associated with thermocline shallowing[22,45] are a potential trigger for the brief vacation and apparent "pre-extinction gigantism" exhibited through Phase 2. The final sample of this species' record may be marked by symbiont bleaching wherein, despite a size increase, specimens exhibit a reduction in $\delta^{13}C$ values (Fig. 1). Alternatively, *D. baroemoenensis* may also be recording rapid migration down to the subsurface, or a significant change in the extent of test calcification just prior to extinction[25,46,47].

Photosymbiont bleaching driven by extreme heat stress has been recorded in extant groups such as corals[48] and larger benthic foraminifera[49,50], and previously, records of the potential bleaching of algal photosymbionts within fossil planktonic foraminifera have been confined to early Cenozoic hyperthermals (e.g., [9,11,18,21,44]). Despite bleaching amongst modern corals being primarily driven by increasing temperatures[48,51,52], a multitude of environmental stressors are associated with bleaching responses[53,54], and the prospective bleaching of *D. baroemoenensis* may indicate that this pre-extinction response in symbiont-bearing taxa may be more common than previously thought during intervals not characterised by elevated temperatures.

Model results (Tables S1-4) lend further support to our interpretations, in which both morphological and ecological responses display discrete signatures between phases, characteristic of disruptive selection[31,32]. The interpreted behaviour of these organisms raises some interesting questions. One of the most pressing and fundamental issues for palaeoceanography, is whether fossil organisms identified via their external morphology which are used for the inference of paleoclimatic data maintain ecological uniformitarianism for the entirety of their stratigraphic range. Our study, alongside other novel research on modern and fossil populations[18,55-64] suggests not, and as such deriving environmental interpretations from fossil taxa, particularly during intervals of climate variability, should be treated with caution. Whether the documentation of these behaviours indicate failed efforts at stress mitigation via water-depth associated parapatric anagenesis is currently undetermined, but further high-resolution comparable investigations through speciation events may help to understand the fundamental mechanisms driving evolution and extinction in an ecosystem with limited vicariance potential such as the open ocean.

5.4 Summary

The studied section exhibits a high-resolution record of the pre-extinction biotic response of two members of the planktonic foraminiferal genus *Dentoglobigerina* during major global palaeoceanographic changes associated with the development of northern hemisphere ice sheet formation. Despite the species' phylogenetic and ecological affinities, documented phenotypic responses are species-specific, wherein both *D. altispira* and *D. baroemoenensis* exhibit evidence of permanent adaptive ecological niche migration and photosymbiont reduction. In addition, *D. baroemoenensis* documents "pre-extinction gigantism", and potential photosymbiont bleaching. This study highlights the importance of high-resolution analyses when investigating biological responses and extinction dynamics. The unparalleled resolution of the marine microfossil record allows us to identify and evaluate past occurrences of morpho-ecological stochasticity indicative of disruptive selection and niche adaptation. However more comprehensive studies utilising multiple localities are required to improve our understanding and identification of the potential for pre-extinction signals to better recognise extinction risk in response to rapid climate change.

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Author contributions

A.D.W, S.L.J, R.A.J, and R.J.N generated the data. All authors contributed to the interpretation of the data. A.D.W plotted figures and wrote the R code to perform statistical analysis. A.D.W and T.A contributed to the writing and editing of the manuscript.

Competing interests

The authors declare no competing interests.

5.5 Methods

5.5.1 Site Selection:

Material was sourced from Integrated Ocean Drilling Program Expedition 321

Site U1338 (Hole 1338A) (2°30.469′N, 17°58.162′W) situated in the East Equatorial Pacific, which was drilled to 410.0 mbsf through Holocene-early Miocene pelagic sediments[65]. At ~3 Ma, the site was in a deep-water pelagic environment of similar water depth and paleolatitude[66] to the modern. The primary lithologies represented are calcareous, diatom and radiolarian nannofossil oozes and chalks. Despite the deep-water settings and primarily calcareous nature of the sediments, excellent microfossil preservation has been recorded throughout this core interval [67]. A preliminary assessment of core U1338A was carried out to determine the approximate position of the extinction of the dentoglobigerinids (~3 Ma) based on tropical biostratigraphy[68], and shipboard paleomagnetic data[65].

5.5.2 Assemblage Analysis:

Sediment volumes of 20-40 cc were collected and washed with de-ionised water over a 63-µm sieve; the residues were dried in an oven at 40 °C and split. All samples were examined using a Zeiss Stemi 305 Compact Stereo Microscope. We identified planktonic foraminifers following the taxonomy of Kennett and Srinivasan[69], Schiebel and Hemleben[28], and Wade et al.[39] and performed assemblage counts on 300 individuals from > 63 µm splits.

5.5.3 Chronology Determination:

During sampling of the extinction interval and identification of the dentoglobigerinid extinction event, specimens of *Cibicidoides wuellerstorfi* were also picked to create a benthic foraminiferal $\delta^{18}O$ record. This record was constructed and tuned to the Ocean Drilling Program Site 849/IODP Site 1338 stack constructed by Lyle et al.[70] using QAnalySeries software[71] to better constrain the timing of pre-extinction responses compared to using palaeomagnetic data alone.

5.5.4 Morphometrics and Repeatability:

The first 50 (where present) complete specimens of the genus *Dentoglobigerina* were picked and mounted in umbilical position on card slides pierced with a fine needle to accommodate the variably spired nature of species in the genus[39]. Specimens were imaged umbilically using a Zeiss Axio Zoom V16 microscope with attached Canon EOS 100D camera at x 19.4 magnification. All specimens were then rotated 90° laterally, and imaged whilst propped onto their penultimate chamber. Images were processed using the image analysis software Image Pro Premier, and the "size" trait parameters: test area (Area, μm^2), and test size range (minimum test diameter (Dmin) - maximum test diameter (Dmax)), and "shape" trait parameters: aspect ratio (AR, ratio between maximum test height and width), roundness (perimeter^2 (μm)/4π.test area), and circularity (4.test area)/($\pi.\text{MaxFeret}^2$), were captured from both orientations, extracted, and databased (see SI). To determine whether the size and shape parameters were repeatably valid measurements, trait repeatability[72,73] was performed by removing, remounting, and reimaging 200 specimens of each analysed dentoglobigerinid species (100 umbilical orientations, and 100 lateral). Measurements of the repeated runs (Fig. S2) are plotted using continuous frequency distributions (kernel density estimates with a Gaussian kernel and bandwidth $h = 1.06*sn^{1/5}$ following Silverman[74], with s the standard deviation of trait measurements per species and n the number of analysed individuals). Results were evaluated through Wilcoxon signed-rank test using R software[75]. Where mean run rank differences deviated significantly, measured traits were deemed non-repeatable (Fig. S3). All measured size and shape trait parameters were deemed repeatable for *D.* altispira, whereas for *D. baroemoenensis*, roundness and circularity were not repeatable, and were subsequently removed from further interpretations. Repeatable traits were then subjected to power analysis[76] using the 'pwr' package in R[77] to determine the minimum number of individuals required to detect mean sample trait changes of 5, 10, 15, 20, 25, and 30% with power > 0.9 and a significance level of $p = 0.01$ as suggested by Brombacher et al.[72] (Fig. S4; Table S5).

5.5.5 Stable Isotope Analysis:

For stable isotope analysis, species-specific size fractions were screened and picked for exceptionally preserved specimens of *Dentoglobigerina altispira* (> 200 µm)*,* and *Dentoglobigerina baroemoenensis* (>200 µm) exhibiting “excellent” and “glassy” preservation[78]*.* The same screening process was performed for nominate taxa representing specific ecological habits through the water column: *Globigerinoides ruber* (212-350 µm, surface mixed-layer), *Neogloboquadrina incompta* (212-350 µm, subsurface), *Globorotalia tumida* (>300 µm, thermocline/photic zone base, corrected for a 1.0‰ $\delta^{13}C$ enrichment due to this species occupying the shallow oxygen minimum zone and consequential effects of reduced ambient pH[25]), *Hirsutella scitula* (212-300 µm, subthermocline), and *Cibicidoides wuellerstorfi* (>212 µm, bottom-water) (see [6,25,79,80]). Single specimens of dentoglobigerinids, and multiple specimens of all other foraminifer species were analysed using an Elementar IsoPrime Dual-Inlet Isotope Ratio Mass Spectrometer in the Cohen Geochemistry Laboratory, University of Leeds, and data are reported to the Vienna Pee Dee belemnite (VPDB) scale using an Elemental Microanalysis Carrera marble standard where analytical precision was better than 0.07 and 0.13 ‰ for $\delta^{13}C$ and $\delta^{18}O$ (1 standard deviation), respectively (Fig. 1 & 3; see SI).

5.5.6 Statistical Analysis

Prior to statistical modelling, all sample mean isotopic and morphometric measurements were log standardised and the sample first differences generated per time step. All statistical analyses and linear modelling were carried out using R software[75]. For linear models, statistically significant relationships were identified between variables, and residual standard mean errors (RSE) were calculated to determine the model fit (Tables S3 & S4). The normality of dentoglobigerinid morphometric and geochemical parameter data was assessed using a Shapiro-

Wilk test[81] to determine whether parametric or non-parametric tests were applicable. Dentoglobigerinid sample-mean morphological and geochemical parameters were tested to identify study section outliers through Grubb's test[26] using the 'outliers' package[82]. Comparisons between all dentoglobigerinid morphological and geochemical parameters between the two phases (i.e., specimens before and after the defined Phase Transition) were performed by Mann-Whitney U[27] using the 'asht' package[83], and z-tests using the 'BDSA' package[84].

Parameter	*D. altispira*	Position	*D. baroemoenensis*	Position
Carbon	0.5492	Within P1	0.07428	Within P1
Oxygen	0.2239	Within PT	0.7708	Within P2
U_Area	***< 0.01***	***Within P2***	***< 0.01***	***Final sample***
U_Aspect Ratio	0.1084	Within PT	0.09192	1st PT sample
U_Dmax	0.07362	Within P2	***< 0.01***	***Final sample***
U_Dmin	***< 0.05***	***Within P2***	***< 0.05***	***Final sample***
U_Range	0.2757	Within P1	0.1778	Within P2
U_Roundness	***< 0.05***	***Within P1***	NA	NA
U_Circularity	0.2506	1st PT sample	NA	NA
L_Area	***< 0.01***	***Within P2***	0.06507	Final sample
L_Aspect_Ratio	***< 0.05***	***Within PT***	0.06467	1st P2 sample
L_Dmax	0.05313	Within P2	***< 0.05***	***Final sample***
L_Dmin	***< 0.01***	***Within P2***	0.264	Penultimate sample
L_Range	0.06445	1st PT sample	0.08086	1st P2 sample
L_Roundness	***< 0.05***	***Last PT sample***	NA	NA
L_Circularity	0.562	Within P2	NA	NA

Table 1. Grubbs' Test results. Bold and italic results indicate statistical significance ($p < 0.05$). U = Umbilical, L = Lateral, P1 = Phase 1, P2 = Phase 2, PT = Phase Transition.

	D. altispira		*D. baroemoenensis*	
Parameter	Test	P1vP2	Test	P1vP2
Carbon	M-W*U*	***< 0.01***	z-test	0.655
Oxygen	M-W*U*	0.183	z-test	***< 0.01***
U_Area	M-W*U*	0.227	M-W*U*	***< 0.01***
U_Aspect_Ratio	M-W*U*	0.806	M-W*U*	0.243
U_Size_Range	M-W*U*	0.557	M-W*U*	***< 0.01***
U_Roundness	M-W*U*	0.135	NA	NA
U_Circularity	M-W*U*	0.937	NA	NA
L_Area	M-W*U*	0.429	M-W*U*	***< 0.01***
L_Aspect_Ratio	M-W*U*	0.272	z-test	0.476
L_Size_Range	M-W*U*	0.227	z-test	***< 0.01***
L_Roundness	M-W*U*	0.506	NA	NA
L_Circularity	M-W*U*	0.176	NA	NA

Table 2. Mann-Whitney U test results for between *D. altispira* and *D. baroemoenensis* phase populations. Bold, italic results indicate statistical significance ($p < 0.05$). U = Umbilical, L = Lateral, P1 = Phase 1, P2 = Phase 2.

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5.7 Supplementary Information

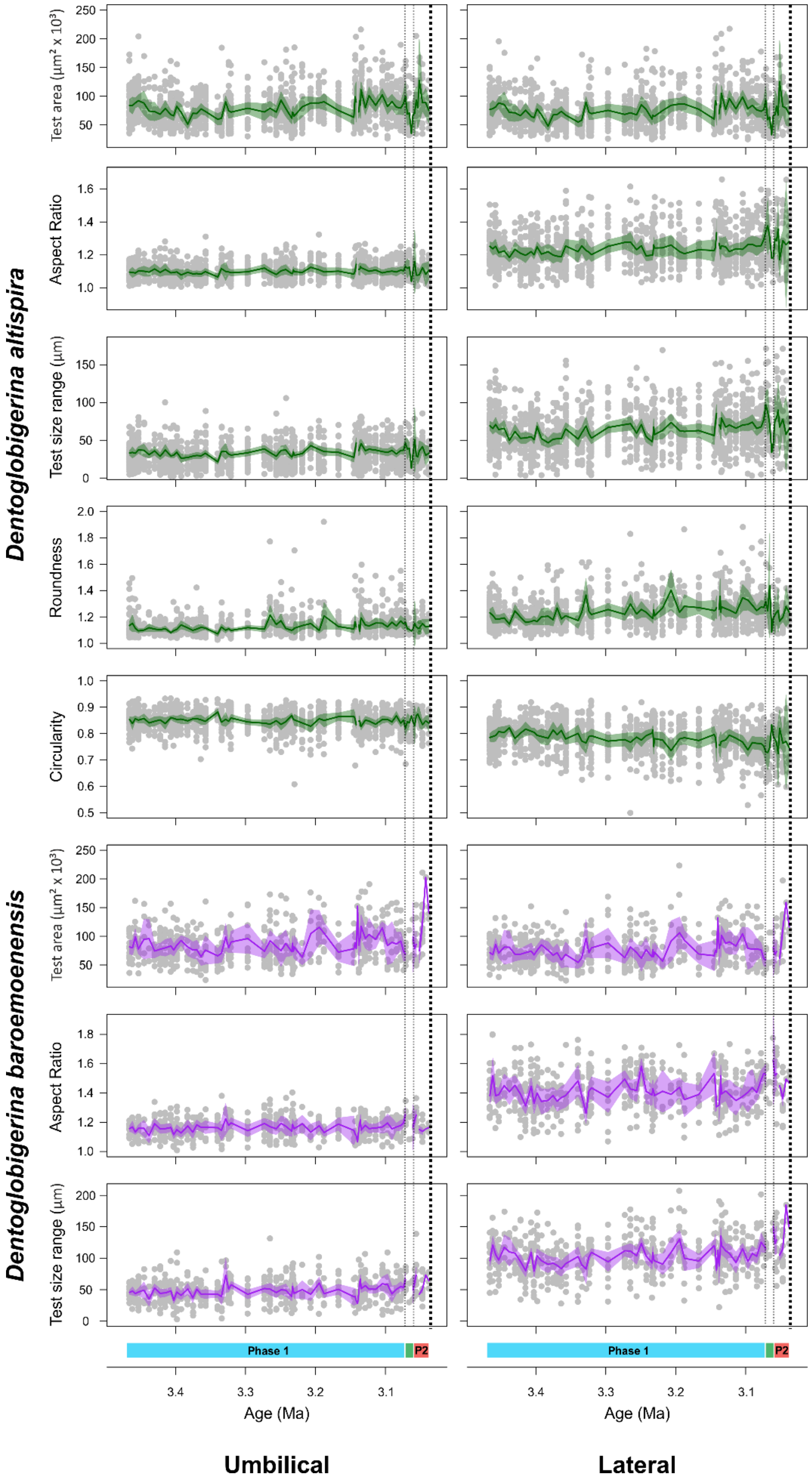

Figure S1. Measured morphometric traits of dentoglobigerinid species. Raw values are plotted as grey dots, mean values as lines and 95% confidence intervals as shaded areas, light vertical dotted lines indicate boundaries between "Phases", black vertical dotted line indicates extinction horizon.

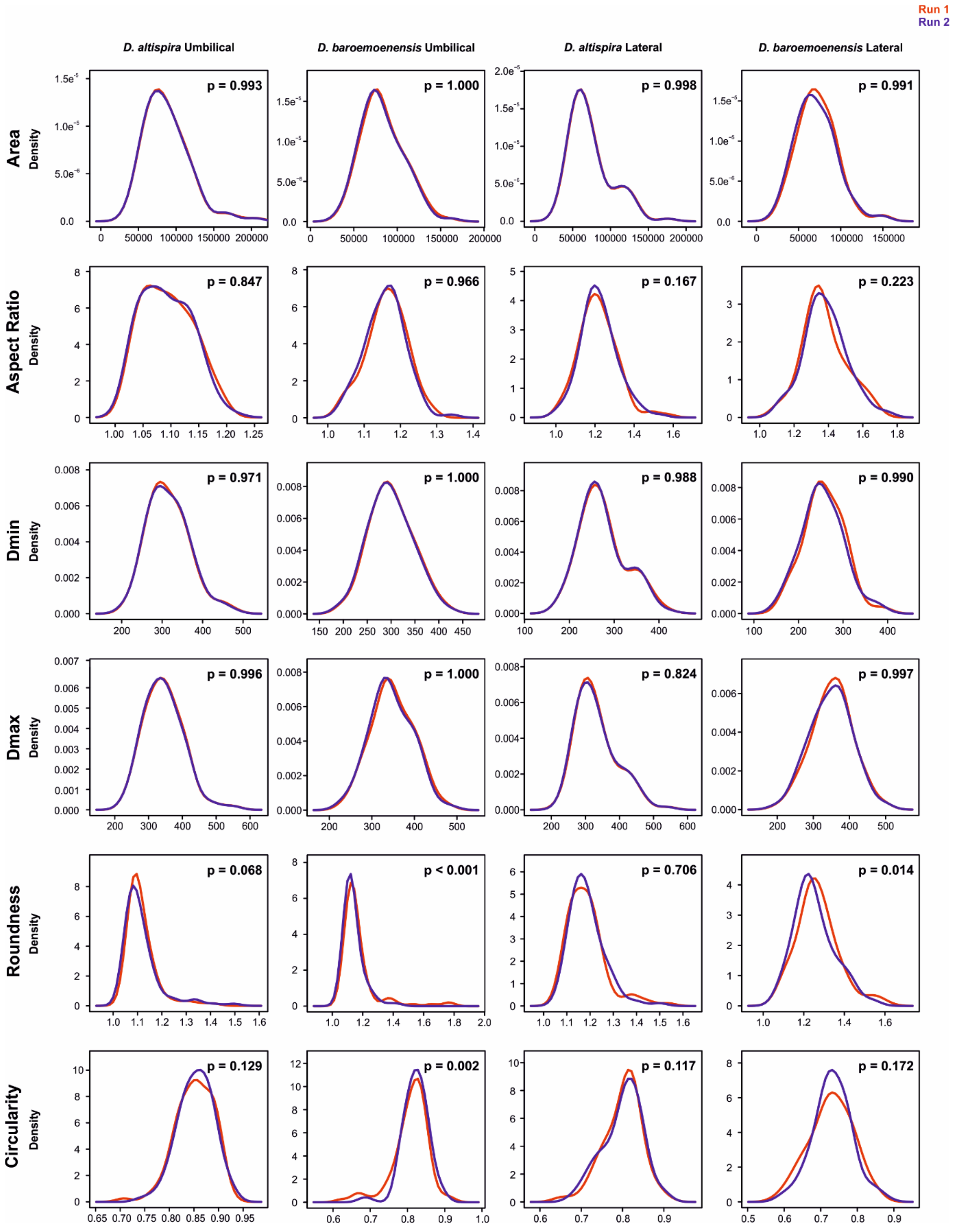

Figure S2. Kernel density plots of first (red) and second (blue) set of morphometric measurements on *Dentoglobigerina altispira* and *Dentoglobigerina baroemoenensis* in umbilical and lateral orientations.

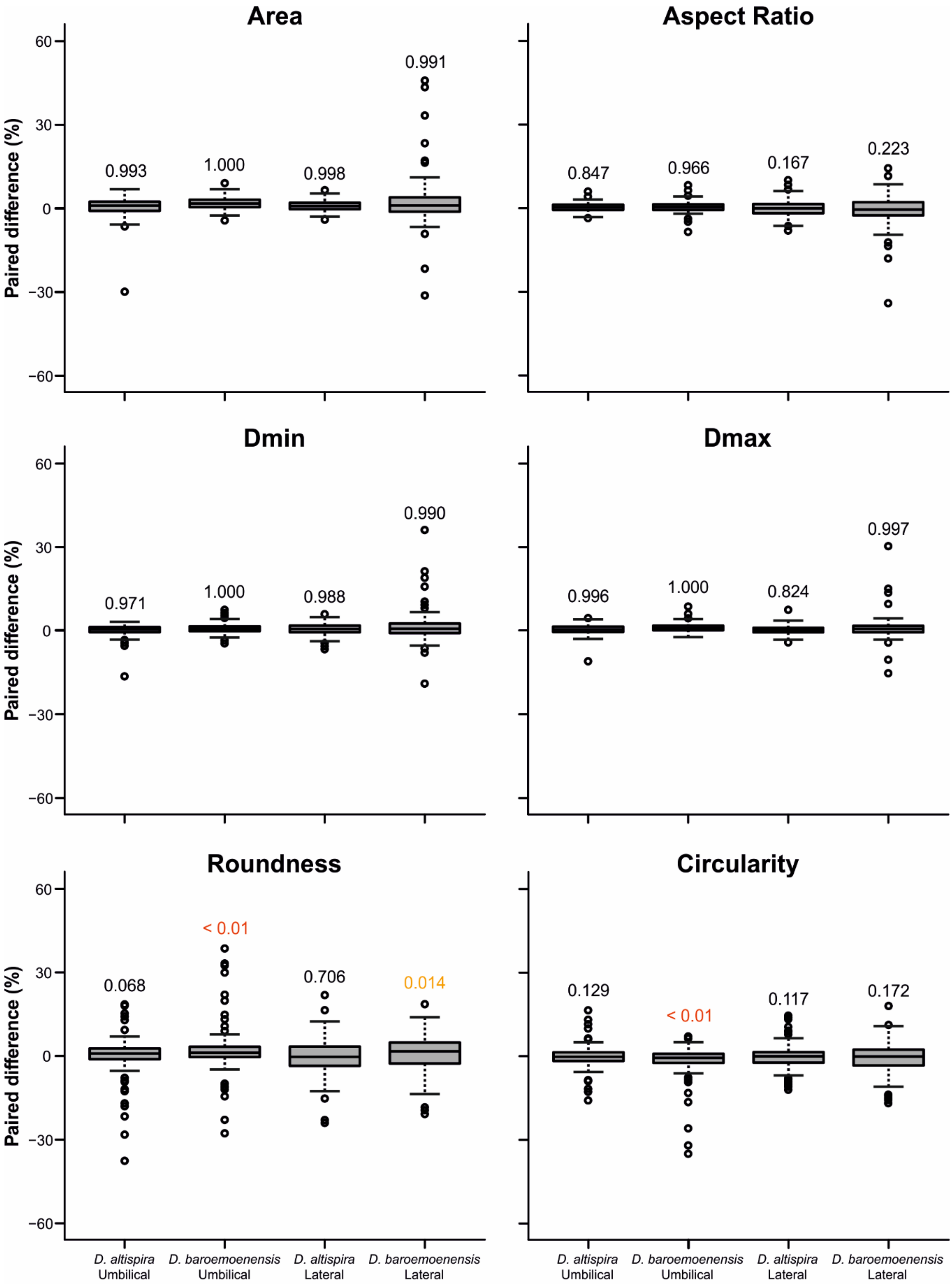

Figure S3. Barplots of the difference between repeated measurements on Area, Aspect Ratio, minimum diameter (Dmin), maximum diameter (Dmax), Roundness, and Circularity on the same individual (paired difference) expressed as percentage of the individual's trait mean. p-values of the Wilcoxon signed-rank test performed on subsequent measurements on the same individuals are given, with p-values < 0.01 & < 0.05 indicating significant differences shown in red and orange, respectively.

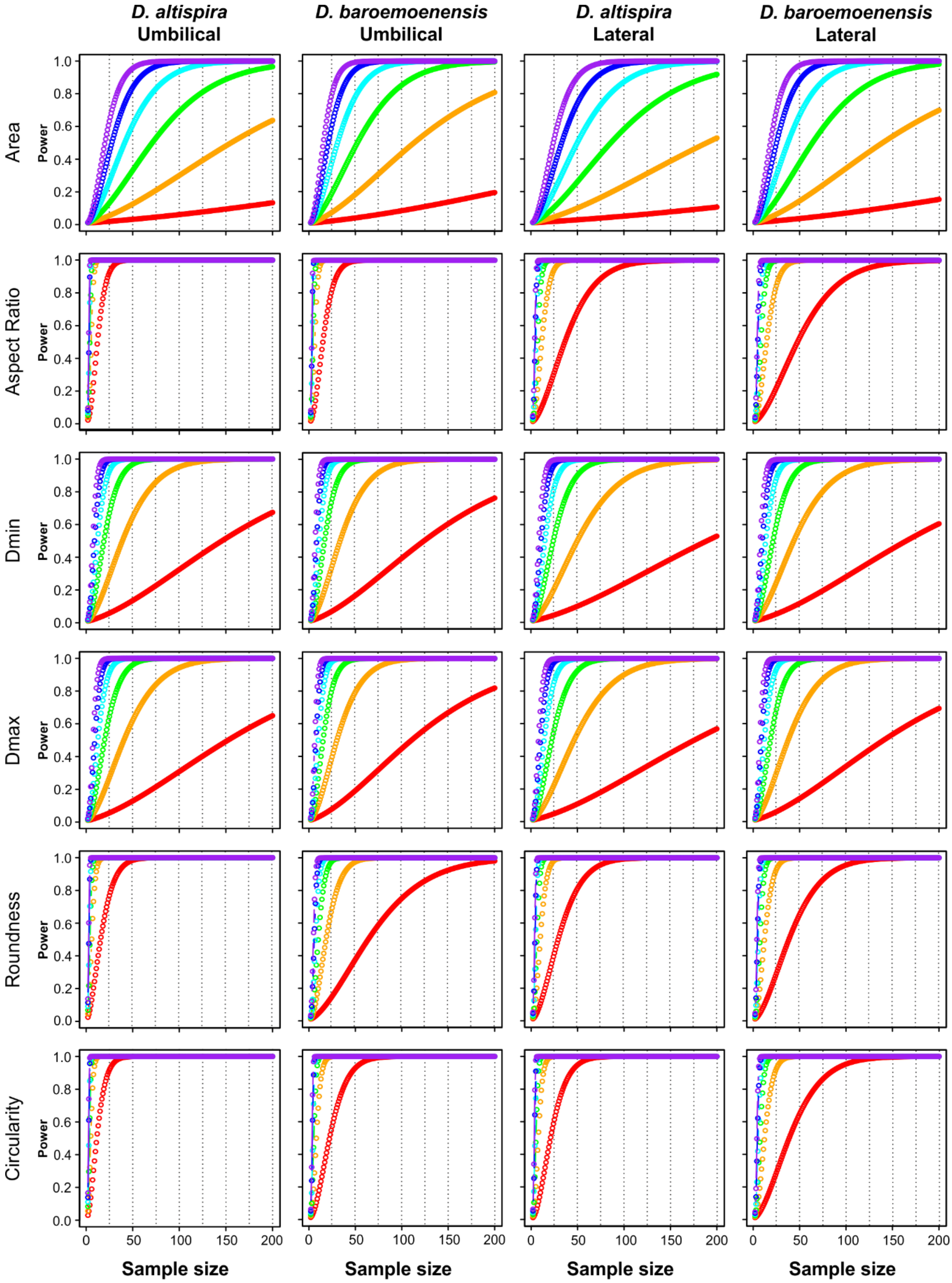

Figure S4. Calibration of the number of induvial specimens required to detect a given trait change in specific orientations. Power is plotted against the number of individuals needed to detect changes in trait values by 5% (red), 10% (orange), 15% (green), 20% (cyan), 25% (blue), and 30% (magenta). Significance is set to $p = 0.01$.

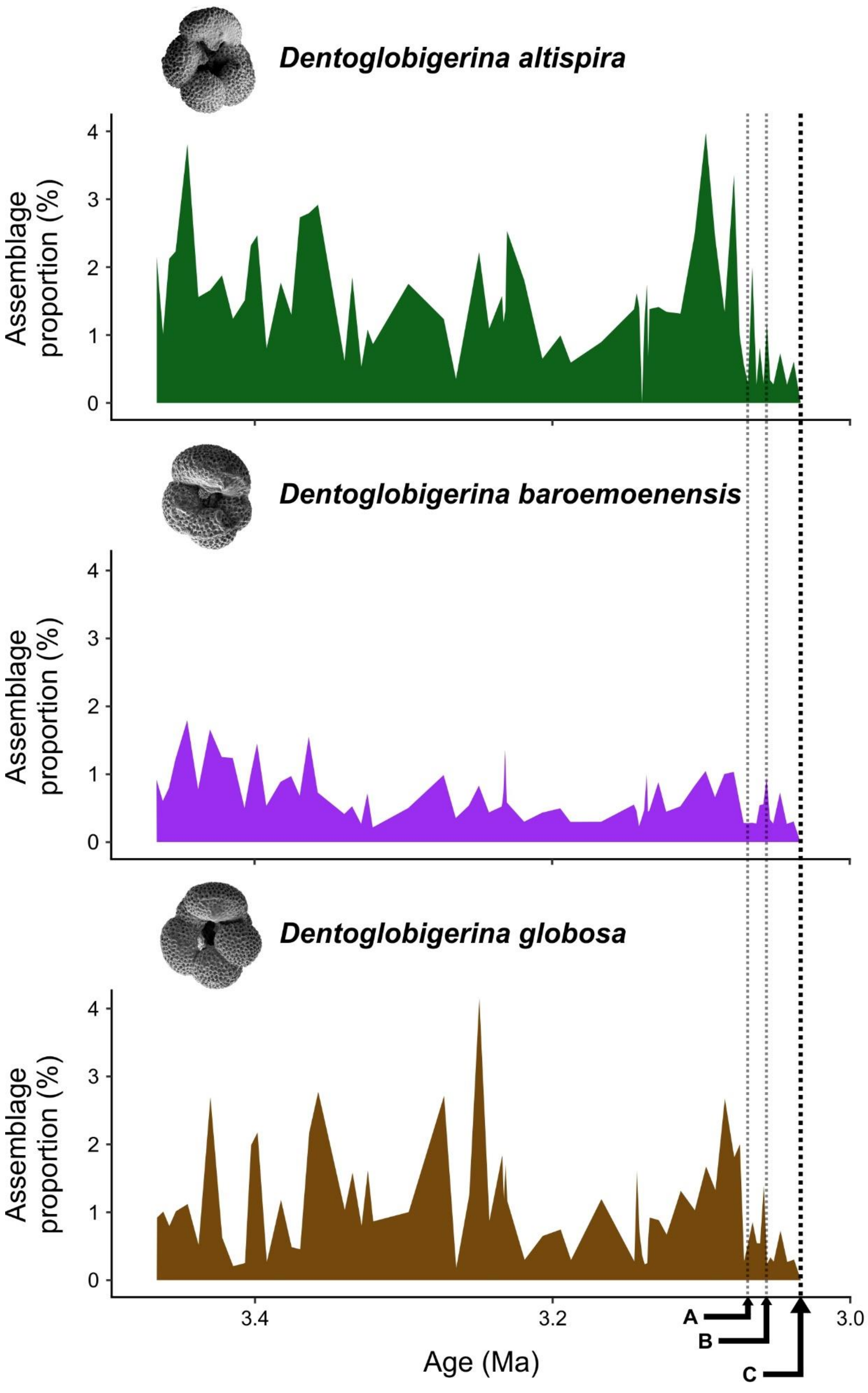

Figure S5. Proportions of species of *Dentoglobigerina* within study assemblage counts, light vertical dotted lines indicate boundaries between "Phases", black vertical dotted line indicates extinction horizon. A = P1-PT boundary, B = PT-P2 boundary, C = extinction horizon.

Table S1. *Dentoglobigerina altispira* LM results for Phase 1

***Dentoglobigerina altispira* LMs**			
Geochemistry vs. geochemistry			
D. altispira ecological signal	Ecological signal	RSE	Correlation
Carbon	*G. tumida* δ^{13}C	28.79	Positive
Carbon	*N. incompta* δ^{13}C	28.86	Positive
Oxygen	*D. baroemoenensis* δ^{18}O	226.06	Positive
Morphology vs. geochemistry			
Trait	Ecological signal	RSE	Correlation
Umbilical Area	*D. baroemoenensis* δ^{18}O	-53.58	Positive
Umbilical Area	*C. wuellerstorfi* δ^{13}C	-51.82	Negative
Umbilical Area	*C. wuellerstorfi* δ^{18}O	-53.35	Positive
Umbilical Area	*G. tumida* δ^{13}C	-54.22	Positive
Lateral Area	*D. baroemoenensis* δ^{18}O	-47.06	Positive
Lateral Area	*C. wuellerstorfi* δ^{13}C	-45.70	Negative
Lateral Area	*C. wuellerstorfi* δ^{18}O	-47.39	Positive
Umbilical Aspect Ratio	*H. scitula* δ^{13}C	-28.32	Positive
Lateral Aspect Ratio	*N. incompta* δ^{18}O	29.23	Negative
Lateral Range	*N. incompta* δ^{18}O	-23.37	Negative
Umbilical Circularity	*G. ruber* δ^{13}C	23.27	Negative
Lateral Circularity	*N. incompta* δ^{18}O	18.69	Positive
D. altispira Morphometry vs. Geochemistry			
D. altispira ecological signal	Trait	RSE	Correlation
Carbon	Umbilical Area	26.54	Positive
Carbon	Lateral Area	26.83	Positive
Carbon	Umbilical Aspect Ratio	NA	
Carbon	Lateral Aspect Ratio	NA	
Carbon	Umbilical Range	27.23	Positive
Carbon	Lateral Range	27.86	Positive
Carbon	Umbilical Roundness	NA	
Carbon	Lateral Roundness	NA	

Carbon	Umbilical Circularity	NA
Carbon	Lateral Circularity	NA
Oxygen	Umbilical Area	NA
Oxygen	Lateral Area	NA
Oxygen	Umbilical Aspect Ratio	NA
Oxygen	Lateral Aspect Ratio	NA
Oxygen	Umbilical Range	NA
Oxygen	Lateral Range	NA
Oxygen	Umbilical Roundness	NA
Oxygen	Lateral Roundness	NA
Oxygen	Umbilical Circularity	NA
Oxygen	Lateral Circularity	NA

Table S2. *Dentoglobigerina baroemoenensis* LM results for Phase 1

***Dentoglobigerina baroemoenensis* LMs**			
Geochemistry vs. geochemistry			
D. baroemoenensis ecological signal	Ecological signal	RSE	Correlation
Carbon	*N. incompta* δ^{13}C	116.58	Negative
Carbon	*N. incompta* δ^{18}O	117.42	Negative
Carbon	*G. ruber* δ^{18}O	117.11	Positive
Oxygen	*D. altispira* δ^{18}O	71.98	Positive
Morphology vs. geochemistry			
Trait	Ecological signal	RSE	Correlation
Umbilical Area	*C. wuellerstorfi* δ^{13}C	64.56	Negative
Umbilical Area	*C. wuellerstorfi* δ^{18}O	66.34	Positive
Lateral Area	*C. wuellerstorfi* δ^{13}C	57.93	Negative
Umbilical Aspect Ratio	*N. incompta* δ^{13}C	-22.61	Negative
Lateral Aspect Ratio	*H. scitula* δ^{13}C	-32.66	Negative
Lateral Aspect Ratio	*G. tumida* δ^{13}C	-30.27	Negative
Lateral Aspect Ratio	*G. ruber* δ^{18}O	-30.88	Positive
Umbilical Range	*N. incompta* δ^{13}C	-31.94	Negative
Lateral Range	*G. tumida* δ^{13}C	-47.80	Negative
Lateral Range	*G. ruber* δ^{13}C	-48.21	Negative
Lateral Range	*G. ruber* δ^{18}O	-48.40	Positive
D. baroemoenensis Morphometry vs. Geochemistry			
D. baroemoenensis ecological signal	Trait	RSE	Correlation
Carbon	Umbilical Area	107.00	Positive
Carbon	Lateral Area	106.66	Positive
Carbon	Umbilical Aspect Ratio	NA	NA
Carbon	Lateral Aspect Ratio	NA	NA
Carbon	Umbilical Range	NA	NA
Carbon	Lateral Range	107.74	Positive
Oxygen	Umbilical Area	NA	NA
Oxygen	Lateral Area	NA	NA

Oxygen	Umbilical Aspect Ratio	NA	NA
Oxygen	Lateral Aspect Ratio	69.012	Negative
Oxygen	Umbilical Range	NA	NA
Oxygen	Lateral Range	NA	NA

Table S3. *Dentoglobigerina altispira* LM results for Phase 2

***Dentoglobigerina altispira* LMs**			
Geochemistry vs. geochemistry			
D. altispira ecological signal	Ecological signal	RSE	Correlation
Carbon	*H. scitula* $\delta^{13}C$	6.11	Positive
Carbon	*H. scitula* $\delta^{18}O$	4.28	Negative
Oxygen	*G. tumida* $\delta^{13}C$	-13.89	Negative
Morphology vs. geochemistry			
Trait	Ecological signal	RSE	Correlation
Umbilical Range	*G. ruber* $\delta^{18}O$	-38.31	Negative
Umbilical Aspect Ratio	*G. ruber* $\delta^{18}O$	-72.35	Negative
Lateral Circularity	*H. scitula* $\delta^{13}C$	1.02	Negative
Umbilical Roundness	*N. incompta* $\delta^{18}O$	-6.15	Negative
Umbilical Roundness	*G. ruber* $\delta^{18}O$	-5.69	Negative
Lateral Roundness	*D. baroemoenensis* $\delta^{13}C$	-3.04	Positive
D. altispira Morphometry vs. Geochemistry			
D. altispira ecological signal	Trait	RSE	Correlation
Carbon	Umbilical Area	NA	NA
Carbon	Umbilical Aspect Ratio	NA	NA
Carbon	Umbilical Range	NA	NA
Carbon	Umbilical Roundness	NA	NA
Carbon	Umbilical Circularity	NA	NA
Carbon	Lateral Area	NA	NA
Carbon	Lateral Aspect Ratio	NA	NA
Carbon	Lateral Range	NA	NA
Carbon	Lateral Roundness	NA	NA
Carbon	Lateral Circularity	NA	NA
Oxygen	Umbilical Area	NA	NA
Oxygen	Umbilical Aspect Ratio	NA	NA
Oxygen	Umbilical Range	NA	NA
Oxygen	Umbilical Roundness	NA	NA

Oxygen	Umbilical Circularity	NA	NA
Oxygen	Lateral Area	NA	NA
Oxygen	Lateral Aspect Ratio	NA	NA
Oxygen	Lateral Range	NA	NA
Oxygen	Lateral Roundness	NA	NA
Oxygen	Lateral Circularity	NA	NA

Table S4. *Dentoglobigerina baroemoenensis* LM results for Phase 2

***Dentoglobigerina baroemoenensis* LMs**

Geochemistry vs. geochemistry

D. baroemoenensis ecological signal	Ecological signal	RSE	Correlation
Carbon	*C. wuellerstorfi* $\delta^{18}O$	3.07	Negative
Oxygen	*D. altispira* $\delta^{13}C$	360.66	Positive

Morphology vs. geochemistry

Trait	Ecological signal	RSE	Correlation
Umbilical Area	*C. wuellerstorfi* $\delta^{18}O$	-2.43	Negative
Lateral Area	*G. tumida* $\delta^{13}C$	-3.58	Positive
Lateral Area	*C. wuellerstorfi* $\delta^{18}O$	-1.69	Negative
Lateral Area	*C. wuellerstorfi* $\delta^{13}C$	-3.21	Positive

D. baroemoenensis Morphometry vs. Geochemistry

D. baroemoenensis ecological signal	Trait	RSE	Correlation
Carbon	Umbilical Area	3.23	Positive
Carbon	Lateral Area	NA	NA
Carbon	Umbilical Aspect Ratio	NA	NA
Carbon	Lateral Aspect Ratio	NA	NA
Carbon	Umbilical Range	NA	NA
Carbon	Lateral Range	NA	NA
Oxygen	Umbilical Area	NA	NA
Oxygen	Lateral Area	NA	NA
Oxygen	Umbilical Aspect Ratio	NA	NA
Oxygen	Lateral Aspect Ratio	NA	NA
Oxygen	Umbilical Range	NA	NA
Oxygen	Lateral Range	NA	NA

Table S5. Power analysis results for dentoglobigerinid size and shape parameters indicating no. of specimens required to detect % change

D. altispira	**% Parameter Change**						
Umbilical	**5**	**10**	**15**	**20**	**25**	**30**	
Aspect Ratio	23	8	6	5	4	4	
Area	1387	345	155	89	58	41	
Dmin	323	83	39	24	16	12	
Dmax	337	87	40	24	17	13	
Roundness	38	12	7	6	5	4	
Circularity	27	9	6	5	4	4	

	% Parameter Change						
Lateral	**5**	**10**	**15**	**20**	**25**	**30**	
Aspect Ratio	78	22	12	8	6	5	
Area	1672	421	189	108	70	50	
Dmin	421	108	50	29	20	15	
Dmax	391	100	46	28	19	14	
Roundness	61	18	10	7	6	5	
Circularity	43	13	8	6	5	4	

D. baroemoenensis	**% Parameter Change**						
Umbilical	**5**	**10**	**15**	**20**	**25**	**30**	
Aspect Ratio	30	10	6	5	4	4	
Area	988	249	113	65	43	31	
Dmin	274	71	33	20	14	11	
Dmax	244	64	30	18	13	10	

	% Parameter Change						
Lateral	**5**	**10**	**15**	**20**	**25**	**30**	
Aspect Ratio	103	28	15	10	7	6	

Area	1225	309	139	80	52	37	
Dmin	366	94	44	26	18	14	
Dmax	311	80	38	27	16	12	

6. Conclusions

6.1 Triton, a new species-level database of Cenozoic planktonic foraminiferal occurrences

The Triton dataset now represents the largest group-specific fossil occurrence dataset ever constructed, allowing for the analysis of macroevolutionary dynamics at a scale never before achieved in science. This collaborative effort will further bolster the Cenozoic planktonic foraminifera as a model-group for the analysis of biological and climatic evolution through deep-time.

6.2 Ecological trends in pre-extinction geographic range trajectories of Cenozoic planktonic foraminifera

Examination of the terminal stratigraphic ranges of Cenozoic macroperforate planktonic foraminifera using the Triton dataset shows that the majority of species exhibit a reduction in geographic range prior to extinction. However, a number of species that evolved within shallower marine waters which host photosymbiotic algae appear to show potential ecological resilience against abiotic selection pressures, as inferred through an increase in their geographic ranges prior to extinction. Amongst major Cenozoic climate events, the most rapid event, the Paleocene-Eocene Thermal Maximum, has the most significant impact on geographic range declines.

6.3 Climate regime drove spatial patterns in speciation and dispersal dynamics of planktonic foraminifera

The use of the Triton dataset to explore the palaeolatitudinal macroevolutionary dynamics within Cenozoic macroperforate planktonic foraminifera reveals that global temperature is the primary environmental driver for the location of speciation palaeolatitudes, where climatic regimes typified by higher mean global temperatures promote speciation in higher palaeolatitudes. Speciation palaeolatitudes have responded to Cenozoic climate, where the general trend of cooling that characterizes the last 50 Myrs is followed by an increase in low-latitude speciation. The vast majority of species first occurrences are consistent with speciation mechanisms facilitated by geographic isolation, as opposed to sympatry, and furthermore, extinction palaeolatitudes tend to be located far from palaeolatitudes of speciation, favouring the contagion hypothesis over the demographic hypothesis.

6.4 Adaptive ecological niche migration does not negate extinction susceptibility

High-resolution investigation of the extinction of two *Dentoglobigerina* species during a period of global cooling revealed species-specific morphological and ecological pre-extinction responses, in spite of the morphological, ecological, and phylogenetic similarities between the taxa. Documented pre-extinction responses include permanent ecological niche migration, pre-extinction gigantism, and algal photosymbiont bleaching, where the latter response has only previously been observed during early Cenozoic intervals of heightened temperature. Rapid phenotypic changes may be a typical feature amongst taxa prior to extinction, however further investigations are needed to establish whether similar behaviour occurs during speciation events.

6.5 Future work

The evolutionary patterns observed within this study yield significant results to advance our understanding of the nature of evolution and extinction within the largest habitat on Earth. The Triton dataset provides a greater capacity than ever before to uncover global scale biotic responses to the secular and transient climatic trends which have shaped the last 66 million years of Earth history. The investigation of pre-extinction responses on multiple spatiotemporal scales appears to support the notion that environmental variability during the evolution of species may promote ecological resilience. Future high-resolution prospecting of planktonic foraminiferal speciation and extinction nodes may eventually reveal whether behaviour comparable to the pre-extinction responses observed in this study are also characteristic of the mechanisms underlying speciation.

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