Marine planktonic microbes survived climatic instabilities in the past

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In the geological past, changes in climate and tectonic activity are thought to have spurred the tempo of evolutionary change among major taxonomic groups of plants and animals. However, the extent to which these historical contingencies increased the risk of extinction of microbial plankton species remains largely unknown. Here, I analyse fossil records of marine planktonic diatoms and calcareous nannoplankton over the past 65 million years from the world oceans and show that the probability of species’ extinction is not correlated with secular changes in climatic instability. Further supporting these results, analyses of genera survivorship curves based on fossil data concurred with the predictions of a birth–death model that simulates the extinction of genera through time assuming stochastically constant rates of speciation and extinction. However, my results also show that these marine microbes responded to exceptional climatic contingencies in a manner that appears to have promoted net diversification. These results highlight the ability of marine planktonic microbes to survive climatic instabilities in the geological past, and point to different mechanisms underlying the processes of speciation and extinction in these micro-organisms.

Keywords: extinction; diversification; marine planktonic microbes; dispersal; climate change; birth–death model

1. INTRODUCTION

Micro-organisms dominate terrestrial, aquatic and aerial ecosystems and largely rule our planet’s life by playing pivotal roles in global biogeochemical cycles [1,2]. Life on Earth is microbe dependent, yet our knowledge about their diversity and evolutionary dynamics is still very limited [2–4]. Historical contingencies such as climatic variations or tectonic events alter local environmental conditions, cause the fragmentation of biomes and threaten the survival of species [5–7]. However, owing to their huge population densities and broad dispersal [8,9], free-living planktonic microbes track changes in global environmental conditions, shift their biogeographic distribution ranges and hence can escape extinction [10–13]. Testing the linkage between climate change and the extinction of microbial plankton species requires the analysis of fossil data with global coverage and over time spans encompassing entire taxonomic lifetimes. This is necessary to eliminate the effect of species’ extinction and subsequent resurgence (Lazarus taxa), a common feature of microbial species. For instance, evidence shows that micro-organisms can revive and thrive after long periods of metabolic quiescence drifting with ocean currents, deposited in deep sea sediments or trapped in polar ice (even for geological epochs) [14,15]. However, most studies on microbial extinction have focused on the analysis of community composition through specific climatic episodes and geographical locations. A few reports have fulfilled the spatial and temporal scale requirements stated above, yet these studies used neither sampling-standardized techniques nor improved mathematical methods for the determination of evolutionary rates, and provided inconclusive results [16–18].

Species’ extinction may respond to different scales of climate variability, including orbital-related climatic oscillations (less than 10^6 years) and long-term variations in radiative forcing (more than 10^6 years) primarily mediated by plate tectonics [6,7,19]. The former alter the geographical distribution of biomes on Earth and are expected to cause attendant variations in the dynamics of extinction, i.e. the larger the climate variability, the higher the extinction probability. In contrast, the latter gradually deteriorate global environmental conditions with respect to living taxa and predict a homogeneous (background) pattern of species’ extinction through time. Additionally, climatic variability and the fragmentation of biomes can reduce the connectivity between populations, promote genetic isolation and consequently enhance the rate of diversification. Here, I use records of climatic variability and microfossil data over the past 65 million years (Myr) from the world oceans and explore the linkage between the rate of climate change and the probability of extinction, origination and net diversification of marine planktonic diatoms and calcareous nannoplankton. First, using sampling-standardized fossil data, I analyse the evolutionary dynamics of these two phytoplankton groups throughout the period of study and compare the results with the climate change record. Second, the evolutionary dynamics at the species level determines the longevity of genera. For instance, if the bulk of species making up a genus are killed, then the genus will go extinct. Conversely, if the number of species in a genus increases, then, according to probability theory, the longevity of the genus will

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increase as well. On this basis, I further test the climate–extinction hypothesis against the predictions of a birth–death (null) model, which simulates the extinction of genera through time assuming stochastically constant rates of speciation and extinction of species.

2. MATERIAL AND METHODS

(a) Fossil data

The dataset of marine planktonic diatoms and calcareous nannoplankton was extracted from the Neptune database, a global record of microfossil occurrences reported by the Deep Sea Drilling Project and Ocean Drilling Programme [20,21]. The complete dataset consisted of 16 896 fossil assemblages (209 117 global occurrences) containing 1914 morphologically defined species (326 genera) collected at 203 sampling sites from the Atlantic, Pacific, Indian and Antarctic Oceans and was downloaded from the Chronos website in July 2008. Sample ages were calculated from biostratigraphic events. This biochronological analysis provides a series of ‘calibrated events’, which mark the first and last appearances of biostratigraphic markers [20,22]. Typically, these biostratigraphic events are correlated in several locations with an independent stratigraphic method, like magnetostratigraphy or oxygen isotope stratigraphy. The fossil record for marine planktonic diatoms and calcareous nannoplankton extended over the past 41 Myr and 65 Myr, respectively.

(b) Climate variability

The climate change record was inferred from a global compilation of δ¹⁸O from deep sea benthic foraminifera [23,24]. The variations in the amplitude of the deep sea δ¹⁸O signal largely reflect on changes in continental ice-volume and global temperature [23]. Once placed in age models, δ¹⁸O data were combined to generate a composite curve from 1 Myr time intervals provides a quantitative estimate of climatic variability that, among other things, is related to Earth’s orbit; the larger the oscillations, the higher the climatic instability that, among other things, is related to Earth’s orbit; the larger the oscillations, the higher the climatic instability. This estimate was calculated by drawing with replacement 12 δ¹⁸O data from each 1 Myr time bin. Then, from each bootstrap dataset, I calculated the maximum oscillation amplitude. Results shown are the mean amplitude from 100 bootstrapped datasets for each time bin. Additionally, the same procedure was carried out separately on independent isotopic records with high temporal resolution (less than 10 000 years).

The long-term trend in climate change was delineated by calculating the difference between the mid-point δ¹⁸O signals from consecutive 1 Myr time intervals. The results were expressed in absolute values (isotopic volatility). The overall pattern is punctuated by specific climatic episodes, such as the Eocene–Oligocene glaciation, and reversals, including the Late Oligocene warming or the Mid-Miocene climatic optimum. Except for some specific events, δ¹⁸O signal gradually increases up to 4‰ between the Late Palaeocene and the present at a relatively constant rate [23]. This gradual increase in δ¹⁸O signal is associated with the drawdown of atmospheric carbon dioxide [23], which was mediated by (i) the uplift of the Tibetan plateau and the ensuing chemical weathering of the exposed rock [26], and (ii) the massive burial of organic carbon during the opening phase of the last Wilson cycle [27,28].

(c) Per capita evolutionary rates

Sampling effort per time interval in the Neptune database is skewed towards recent records. To eliminate biases related to unequal sampling intensity across time intervals, the rates of extinction and origination were calculated using sampling-standardized fossil data [29]. One hundred independent datasets were generated by sampling a fixed number of taxonomic lists from each 1 Myr time bin. The sampling quotas were 9 samples for diatoms and 31 samples for calcareous nannoplankton. These sampling quotas were defined as the maximum number of samples that enabled the calculation of the probability of extinction and origination for all time bins containing fossil data. For each replicate dataset, I determined the dates of the first and last occurrence for each taxon. Then, the estimates of per capita extinction (R_e) and origination (R_o) rates were calculated as the natural log of the ratio of taxa that range through a time bin to either that only cross the bottom boundary of the bin (for extinction), R_e = −ln(N_o/N_t)/Δt, or those that only cross the top boundary (for origination), R_o = −ln(N_o/N_t)/Δt. In these equations, N_o is the total number of taxa crossing the bottom boundary of the time bin, N_t is the total number of taxa crossing the top boundary, N_o is the total number of taxa that cross both boundaries and Δt is the duration of each time bin [30]. Results shown are mean extinction and origination rates from 100 replicate datasets. Diversity estimates, calculated by applying the lists unweighted method for sampling standardization, were extracted from Rabosky & Sorhannus [3].

Evolutionary rates at the beginning and the end of the time series can be biased by edge effects. Taxa with last occurrence dates near to recent times might not be extinct. This generates an artefactual increase in the rate of extinction for recent time intervals [30]. The same occurs with the rate of origination but for the oldest time intervals; taxa with first occurrence dates in the database could appear earlier. Therefore, the rates of extinction and origination were constrained, respectively, to times before the Pliocene epoch and later than the Late Eocene for planktonic diatoms and Late Palaeocene for calcareous nannoplankton.

A potential problem with the estimates of first and last occurrence dates is related to the observation that there is a time lag between species’ origination, extinction and their maximum geographical occupancy [31]. The probability of sampling a species depends on its geographical distribution and consequently this will vary through the lifetime of the species. Thus, first and last occurrence dates in the Neptune database could be biased by this phenomenon. However, assuming that the periods of rise and fall are relatively similar among species originating at a given time, my initial (null) hypothesis that the probabilities of origination and extinction are independent of climatic variability should remain testable.

Per capita rates of extinction and origination were correlated against climatic instability (i.e. the amplitude of δ¹⁸O in 1 Myr time intervals). Cross-correlations, in which time series are correlated applying time-lags between variables, were also performed (electronic supplementary material, figure S1).

(d) Birth–death model

The model is analogous to a pure birth–death process in population biology [32,33]. Rates of speciation and extinction quantify the probabilities that a speciation or
extinction event will occur within a particular time interval \((t)\). The average size of a clade or genus, \(E(n)\), changes as \(E(n) = \exp^{bt-dt}\), where \(b\) and \(d\) are speciation and extinction rates, respectively, and \(t\) is the time interval. Assuming that evolutionary rates are constant, then the probability, \(P(n)\), that a genus survives by time \(t\) is

\[
P(n > 0\,|\,t) = 1 - \frac{bt}{1 + bt} \quad \text{if } b = d
\]

and

\[
P(n > 0\,|\,t) = 1 - \frac{d(\exp^{(b-d)t}) - 1}{b(\exp^{(b-d)t}) - d} \quad \text{if } b \neq d,
\]

where \(n(i)\) is the number of species containing the genus at a given initial time [32,33]. In this model, genera containing one single species will go extinct first, then genera with two species, three and so on.

I tested the null hypothesis that the extinction of marine planktonic diatoms and calcareous nannoplankton followed a stochastically constant extinction pattern. The null model was built upon the birth–death model described above. Then, the model output was tested against dynamic survivorship curves of genera generated from fossil data. In contrast to cohort analysis, dynamic survivorship analysis considers the ensemble of taxa present within a given time interval, no matter what time they originated (pseudocohort). Cohort analysis is generally preferred because it does not rely on the assumption of a stable age distribution; however, as opposed to dynamic survivorship analysis, it requires a large dataset. In this study, generic extinction was examined by applying the dynamic survivorship method.

The model generates genera survivorship curves by choosing randomly (i) the species per genus distribution of the pseudocohort at a given time, and (ii) the rates of speciation and extinction of species (see electronic supplementary material, figures S2 and S3 for details). Speciation and extinction rates were chosen at random within a narrow range of observations (0.05–0.08 per species per million years). These evolutionary rates set the limits of the stochastically constant extinction scenario. Deviation of fossil data from model predictions would be indicative of either rapid radiation or massive extinction. Note that only pre-existing genera are included in the survivorship analysis.

### 3. RESULTS

The variations in the oscillation amplitude of the deep sea \(^{18}\)O signal largely reflect on changes in continental ice-volume and global temperature [23] which, to first order, control the strength of the poles-to-equator heat gradients, ocean physics and chemistry, and hence the spatial and temporal distribution of autotrophic plankton. These isotopic variations provide a quantitative estimate of climatic instability, with the lowest amplitudes recorded in the Late Eocene prior to the onset of permanent Antarctic ice-sheets, and larger amplitudes in the Late Oligocene, Early Miocene and Pleistocene linked to periods of partial and full glaciation (figure 1a). In the long term, Earth’s climate has experienced a gradual shift through most of the Cenozoic, drifting from warm, ice-free periods to glacial periods of extreme cold at a relatively constant rate [23] (figure 1b).

Evolutionary rates were remarkably low and constant throughout the period of study (figure 1c–f). On average,

\[
\text{Per capita extinction rates were } 0.06 \pm 0.03 \text{ (± s.d.) and } 0.06 \pm 0.02 \text{ per species per million years for planktonic diatoms and calcareous nannoplankton, respectively,}
\]

and were not correlated with secular changes in climatic instability. Per capita origination rates were 0.07 ± 0.04 per capita extinction rates were 0.06 ± 0.03 (± s.d.) and 0.06 ± 0.02 per species per million years for planktonic diatoms and calcareous nannoplankton, respectively.

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**Figure 1.** Evolutionary dynamics of marine phytoplankton. (a) Climatic instability calculated from the whole deep sea \(^{18}\)O dataset (grey line) and from individual isotope records with time resolution < 10 000 years (coloured lines). The running mean using the ensemble of data is also shown (black line). (b) Rate of long-term climate change (isotopic volatility). (c) Per capita extinction rate of marine planktonic diatom species and genera (thick and thin lines, respectively). (d) As (c) but for calcareous nannoplankton. (e) Per capita origination rate of marine diatom species and genera (thick and thin lines, respectively). (f) As (e), but for calcareous nannoplankton. (g) Net diversification rate of diatoms (red) and calcareous nannoplankton (blue). (h) Diversity dynamics of diatoms (red) and calcareous nannoplankton (blue) [3]. The arrows on the diversity curves indicate the beginning of diversity declines. LPTM, Late Palaeocene Thermal Maximum; ECO, Eocene Climatic Optimum; EOG, Eocene–Oligocene Glaciation; DPO, Drake Passage Opens; OMG, Oligocene–Miocene Glaciation; MMCO, Mid–Miocene Climatic Optimum. P, Eo, O, M and Pl are Palaeocene, Eocene, Oligocene, Miocene and Plio/Pleistocene, respectively.
and 0.07 ± 0.03 per species per million years, respectively, and neither responded to enhanced climatic instability (figure 1e,f). However, my analysis highlights periods characterized by a higher rate of net diversification linked to climatic episodes occurring across the Late Palaeocene–Eocene and the Eocene–Oligocene boundary transitions (figure 1g). These evolutionary patterns were consistent with the temporal dynamics of diversity (figure 1h). For instance, the loss of diatom diversity across the Oligocene was associated with a decrease in the rate of origination rather than with changes in the probability of extinction, which remained relatively homogeneous. The same evolutionary pattern explained the gradual loss of diversity of calcareous nannoplankton through the Late Eocene–Early Miocene (figure 1a). Interestingly, a depiction of evolutionary rates ranked in order of decreasing magnitude shows that periods of higher evolutionary activity were associated with pulses of origination and net diversification, yet extinction seems to have dominated evolutionary turnover at background levels (figure 2), gradually decreasing global diversities.

To further test the climate–extinction hypothesis, I constructed genera survivorship curves from fossil data and compared the results with the predictions of a birth–death model [32,33]. In this model, the rates of speciation and extinction quantify the probability that a speciation or extinction event will occur within a particular time interval, and then, on the basis of probability theory, the model calculates the percentage of genera that survive through time (see §2 and the electronic supplemental material for additional details). For instance, an increase in the rate of speciation will increase the longevity of genera by adding new species to their pool. Conversely, an increase in the rate of species’ extinction would lead genera to a rapid demise, and therefore to a shortening of their lifetime. In each model simulation, the rates of speciation and extinction were chosen at random within a narrow range of observations, which set the limits of the null model; that is, the stochastically constant extinction scenario (figure 3). Figure 3 shows dynamic survivorship curves of genera from fossil data and the model simulations. The birth–death model reproduced reasonably well the pattern of generic survivorship depicted from fossil data. There were not remarkable deviations either negative or positive with respect to model predictions. Therefore, the null hypothesis that the dynamics of extinction of these marine microbes followed a homogeneous (background) pattern of species extinction through time cannot be rejected.
boundary transitions caused substantial morphological diversification. This signature is not manifest in the analysis of generic survivorship curves almost certainly because to a large extent these arising species were classified as new genera. It must be noted that only the evolutionary dynamics of species in pre-existing genera is considered in the survivorship analysis.

The observation that the rates of extinction and origination of microbial plankton species followed different response patterns suggests that these evolutionary processes were controlled by different mechanisms or by the same mechanisms but operating over distinct temporal and spatial scales (figure 2). In asexually reproducing micro-organisms, single-cell mutations and natural selection can promote rapid speciation under changing environmental conditions and strong selective pressures [36]. However, the extinction of a species implies that all individuals within the entire (often panmictic) population are killed. For marine planktonic microbes with enormous dispersal ranges and potential to maintain viable populations for long time, extinction is likely to be dependent on ubiquitous and prevalent forces either biotic or abiotic that gradually cause habitat loss at a global scale.

Interspecific competition is one of the most prominent causes of extinction. Classical competition theories predict that species competing for the same suite of limiting resources cannot coexist, and ultimately the superior competitor will drive all other species to extinction. Counterbalancing the impact of this biological pressure, theoretical models and experimental results suggest that tradeoffs between species in terms of their abilities to compete for resources and their potential for dispersal can facilitate the coexistence [37]. For instance, inferior competitors evolve dispersal mechanisms that allow them to move to sites where interspecific competition is weaker and hence prosper at different times and places [37]. However, microbial species, and more specifically those inhabiting plankton ecosystems such as marine planktonic diatoms and calcareous nannoplankton, possess enormous dispersal ranges [8,9] and as a result they cannot escape permanently from their competitors. This fact might limit the efficiency of dispersal-competition tradeoffs in marine planktonic microbes and suggests that the pervasiveness of biological pressures over evolutionary time scales could be a primary driver of the extinction of these micro-organisms.

The fundamental reasons for the rapid radiation of these marine phytoplankton are poorly understood. The increase in diatom diversity at the end of the Eocene could be associated with the expansion of grasses on land. This phenomenon accelerated the remobilization of silica from continents, and hence increased the oceanic inventory of this essential nutrient for diatoms [38]. Unfortunately, the precise timing of the expansion of grasses on land remains poorly constrained. Indeed, it has been suggested that the expansion of grasses could have occurred later in the Miocene, negating a causal relationship between the explosive diversification of diatoms at the end of the Eocene and the enhancement of silica fluxes from the continents to the ocean [3]. Aside from the silica hypothesis, the cooling event at the Eocene–Oligocene boundary transition enhanced upper ocean turbulence and the supply of nutrients to the surface layers. Diatoms are a group of fast-growing species that respond to elevated inputs of mineral nutrients [39], and therefore, this climatic contingency could facilitate their diversification. On the other hand, changes in ocean chemistry and the increase of global temperature and ocean stratification across the Late Palaeocene–Eocene boundary transition could have promoted the diversification of calcareous nannoplankton, a group of organisms adapted to inhabit calm ocean waters [18]. This burst of diversification in part could be favoured by the availability of empty niches during a period in which the levels of global diversity had not fully recovered from the Cretaceous–Tertiary extinction event.

The implications of my results are limited to the linkage between climatic variability and the evolution of microbial plankton over the past 65 Myr. It is well known that other contingencies, such as bolide impacts or dramatic biogeochemical episodes that occurred earlier in the history of Earth, suddenly eliminated specific habitats from the globe, profoundly altered biotic interactions and caused massive extinctions in the microbial plankton [40–42]. My results do not preclude a role for massive extinction events as determinants of the evolutionary trajectories and diversity dynamics of marine planktonic microbes in the past. However, to the extent that contemporaneous trends in climate change have analogies with the climates of the geological period analysed here, my results suggest that these microbial plankton groups will persist in the future ocean, perhaps even expanding their ranges of morphological diversity.

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Evolutionary dynamics of microbes


