Research paper

Diversification patterns of planktic foraminifera in the fossil record

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ABSTRACT

Theories of taxonomic diversification dispute whether global diversity has an upper limit set by the strength of biological interactions or grows in unlimited fashion until catastrophic events reset the system. We analyzed a global compendium of fossil planktic foraminifera from the early Cretaceous to the present after correcting for temporal differences in sampling effort. Our results show that their morphological diversity has increased exponentially through time in two different phases. The first phase collapsed at the Cretaceous–Paleogene boundary transition. The second phase developed through the Cenozoic era and declined during the Pliocene–Pleistocene interval, a period of time that was dominated by enhanced climatic and oceanographic instability. In none of these phases diversity reached an equilibrium level. Cenozoic faunas evolved faster than those inhabiting Cretaceous oceans, perhaps as a result of a higher environmental variability. Our results indicate that planktic foraminifera conform to an exponential diversification model. However, because catastrophic events have repeatedly reset the level of biological diversity and have kept it below the maximum, we cannot confirm whether the level of diversity is potentially unlimited.

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1. Introduction

The number of taxa changes through evolutionary time, yet the patterns and causes of these changes remain an open question in micropaleontology (Berggren, 1969; Stanley et al., 1988; Knoll, 1994). Based primarily on the metazoan fossil record, two models of clade diversification, equilibrium and non-equilibrium models, have been proposed to explain the evolution of taxonomic diversity since the Cambrian (Raup, 1976; Alroy et al., 2008; Benton, 2009). The equilibrium model is based on Darwin's ideas that biological interactions such as competition and predation shape the diversity of life (Van Valen, 1973). This view of diversity dynamics mathematically conforms to a density-dependent function such that diversity rapidly increases at the beginning, during the colonization stage, until it reaches a saturation level or carrying capacity (Fig. 1, the logistic model). At equilibrium, the origination and settling of new species are balanced by the failure and extinction of earlier taxa in what has been termed an evolutionary arms race (Van Valen, 1973). Other paleontologists see evolution differently and hypothesize that abiotic, extrinsic controls drive evolutionary turnover (Valentine and Moores, 1972; Benton, 1987). In this scenario, taxonomic diversity increases following an exponential diversification model, which eventually is truncated by catastrophic, unpredictable events such as the impact of asteroids, enhanced volcanic activity, climatic contingencies or shortage of food supply. Among the proponents of the exponential diversification model, two alternative schools of thinking can be further distinguished, i) those who think that diversity is indeed unlimited (Fig. 1, the exponential model), and ii) those who think that there is an upper limit, which, however, is rarely reached because external crises reset the level of biological diversity and keep it below the maximum (Benton, 1987) (Fig. 1, the truncated model).

Our ability to elucidate whether diversity evolves through time according to equilibrium or non-equilibrium theories is limited by the incompleteness of the fossil record (Sepkoski, 1976; Signor, 1978; Alroy et al., 2001). For instance, the availability of sedimentary packages decreases with the time elapsed since their deposition, and consequently the number of taxonomic lists in global fossil compendia typically increases towards recent times. This sampling bias has led to the suggestion that exponential diversification models might be the result of incorrect interpretations of data (Raup, 1976; Sepkoski, 1976; Alroy et al., 2008). To circumvent this limitation, paleontologists have adopted alternative tools based on species re-sampling and rarefaction curves aimed at making diversity estimates from disparate geological time periods comparable (Alroy et al., 2001). The new, corrected curves of marine animal diversity fail to show an exponential diversification pattern, which is replaced by the observation that global diversity
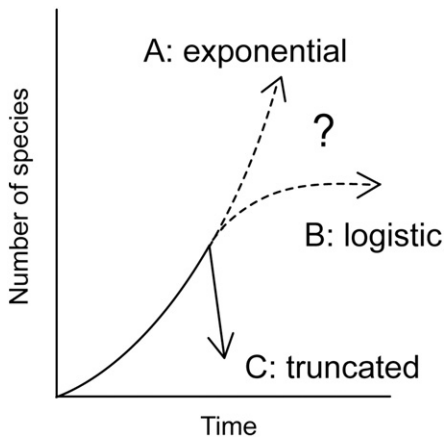
Fig. 1. Theoretical models of biological diversification. (A) Exponential diversification model in which diversity rises unbounded. (B) Equilibrium model in which diversity rises at the beginning until it reaches a saturation level imposed by the strength of biological interactions. (C) Exponential diversification model truncated by the impact of catastrophic events. The occurrence of these catastrophic episodes limits our ability to identify whether diversity dynamics holds to an exponential or equilibrium model.

stabilizes after the mid-Cretaceous (Alroy et al., 2008). However, the extent to which these methods of sampling standardization provide an unbiased picture of diversity dynamics remains controversial in the light of phylogenetic evidence (Benton, 2009).

Few studies have explored the diversity dynamics of microorganisms using sampling standardized fossil data; i.e. data corrected for differences in sampling effort through time. The diversity trajectories of marine planktonic diatoms and calcareous nannoplankton have been corrected by applying methods of sampling standardization (Rabosky and Sorhannus, 2009; Lloyd et al., 2012a,b). The diversity trajectories reported for these two groups of autotrophic microplankton underscore instances of rapid diversification linked to episodes of climate change and reorganization of ocean circulation patterns. However, the relatively short time span of these time series and the occurrence of historical contingencies such as the onset of the Antarctic circumpolar current, which apparently led to a major decrease of siliceous plankton during the Oligocene, precluded identifying the mode of microbial plankton diversification.

The foraminifera are a group of amoeboid heterotrophic protists which are common in plankton ecosystems throughout the world oceans. Planktic foraminifera produce elaborate skeletons of calcium carbonate that have constituted a major component of the microzooplankton fossil catalog since the early Jurassic (Hart et al., 2003). Their extraordinary fossil record at the morphospecies level and high temporal resolution (tens of thousands of years) through much of the time series is unprecedented. Here, we use data of planktic foraminifera fossils spanning the last 120 million years to investigate their diversity dynamics and evolutionary rates. It has been suggested that exponential diversity trajectories might be the result of differences in sampling effort across the time series (i.e., the number of samples increases towards the present). Our analysis was performed using sampling standardized fossil data and occurrences instead of range data for the estimation of speciation and extinction rates. Sampling standardization was conducted by taking the same number of samples per time bin across the time series. This methodological procedure removes biases related to i) unequal sampling effort across the time series, and ii) edge effects such as the Pull of the Recent or the Signor–Lipps effect (Signor and Lipps, 1982; Foote, 2000; Alroy, 2008), that cause smearing of rates before a large sampling spike or across mass extinction events. We compare our diversity curves with those generated using alternative analytical methods and discuss the extent to which these curves support equilibrium or non-equilibrium diversification theories.

2. Material and methods

2.1. Data

The dataset of planktic foraminifera was extracted from the Neptune database, a global record of microfossil occurrences reported by the Deep Sea Drilling Project and Ocean Drilling Program. The dataset was downloaded from the Chronos website (http://services.chronos.org/databases/NEPTUNE/index.html). Synonymies were corrected using information available on PlankRange (http://palaeo.gly.bris.ac.uk/Data/plankrange.html) and TaxonConcept (http://taxonconcept.stratigraphy.net/). Occurrences not identified at the species level and taxa with fewer than five occurrences in the database were removed. The final dataset consisted of 123,714 global occurrences, meaning presence of a taxon in a sample. We used a total of 9843 samples containing 698 morphologically-defined species collected at 152 sampling sites in the Atlantic, Pacific and Indian oceans. Biostratigraphic age attributions in several locations are confirmed using an independent stratigraphic method, like magnetostratigraphy or oxygen isotopic data. The dataset extended over the past 120 million years. Data were binned into intervals of 1 million year in duration.

The Cenozoic record in the database is supported by recent revisions of species taxonomy and by the large recovery of Cenozoic successions worldwide. However, the inventory of Cretaceous species from the database has not been updated yet; i.e. lots of synonyms were not corrected and several newly erected species and genera are not included. In principle, these taxonomic biases could influence the comparison of diversity dynamics between the Cenozoic era and the Cretaceous. However, overestimated numbers of species in the Cretaceous would not change the pattern. Thus, in spite of the problems mentioned above, the general trends presented should faithfully record the history of diversity dynamics of planktic foraminifera since the early Cretaceous.

2.2. Sampling standardization

Sampling effort per time interval in the Neptune database is skewed towards recent records (Fig. 2). To correct for differences in sampling effort across the time series, our estimates of diversity and evolutionary rates were calculated from sampling-standardized fossil data. We used the lists unweighted, sub-sampling method, which randomly draws a fixed quota of samples per time interval (Alroy et al., 2001). The sampling quota was 14 samples. Next, diversity, speciation rate and
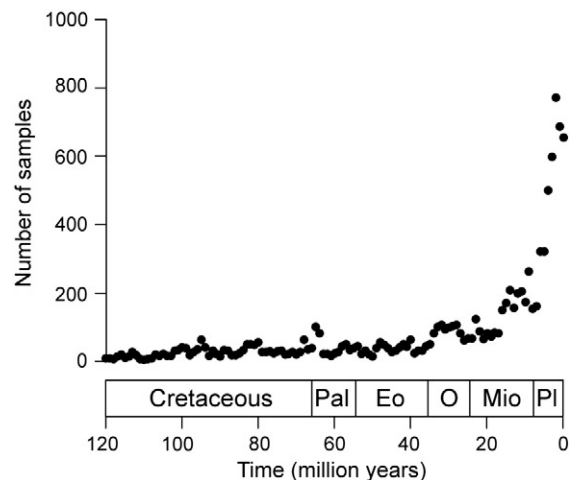
Fig. 2. Number of foraminiferal samples per million year in Neptune database. A sample is defined as a list of taxonomic occurrences associated with a particular horizon in a particular drilling core.