A model for global diversity in response to temperature change over geological time scales, with reference to planktic organisms

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HIGHLIGHTS

- Biotic and abiotic factors are both important in the mortality of populations and species extinction.
- We devise a numerical model to simulate the mutual effect of environmental fluctuations and competition.
- We focus on temperature as the environmental variable and compare model prediction with freely dispersive organisms (planktic).
- Model highly adjustable for future paleobiological and ecological applications.

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ABSTRACT

There are strong propositions in the literature that abiotic factors override biotic drivers of diversity on time scales of the fossil record. In order to study the interaction of biotic and abiotic forces on long term changes, we devise a spatio-temporal discrete-time Markov process model of macroevolution featuring population formation, speciation, migration and extinction, where populations are free to migrate. In our model, the extinction probability of these populations is controlled by latitudinally and temporally varying environment (temperature) and competition. Although our model is general enough to be applicable to disparate taxa, we explicitly address planktic organisms, which are assumed to disperse freely without barriers over the Earth's oceans. While rapid and drastic environmental changes tend to eliminate many species, generalists preferentially survive and hence leave generalist descendants. In other words, environmental fluctuations result in generalist descendants which are resilient to future environmental changes. Periods of stable or slow environmental changes lead to more specialist species and higher population numbers. Simulating Cenozoic diversity dynamics with both competition and the environmental component of our model produces diversity curves that reflect current empirical knowledge, which cannot be obtained with just one component. Our model predicts that the average temperature optimum at which planktic species thrive best has declined over the Neogene, following the trend of global average temperatures.

1. Introduction

Both biotic and abiotic factors, as well as their interplay, are thought to contribute to driving macroevolutionary and macroecological processes on time scales of millions of years (Ezard et al., 2011; Liow et al., 2011), although abiotic forcing is thought to be dominant (Benton, 2009). The detailed mechanics of how species ecologies affect their interactions with other species and their abiotic environment may be clade-, species- (Ezard et al., 2011; Lorenzen et al., 2011) or

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even population-specific. The combination of species idiosyncrasies and environmental stochasticity gives rise to varying patterns and processes of the unfolding of organismal diversity over time. No two clades show the same pattern of waxing and waning over geological time scales, even when they have been exposed to the same global environmental changes (Blois and Hadly, 2009; Foote, 2000). Similarly, members of the same clade in different regions of the globe may not respond to global changes in the same way (compare Meloro et al., 2008; Quinteros et al., 2004).

Despite the complexity of the processes underlying the empirical diversity patterns, there is value in creating relatively simple models to examine mechanisms that drive species richness. We use this approach in order to study how both abiotic (temperature) and biotic (competition) factors might control the macroecological and macroevolutionary dynamics of freely migrating species over geologic time scales. This modelling approach complements empirical comparisons of estimated taxon richness and their putative drivers with paleoclimatic timeseries (Alroy et al., 2000; Hannisdal and Peters, 2011; Mayhew et al., 2008).

Here, we focus on temperature and competition as drivers of the dynamics of populations, which allows us to keep our model tractable. Temperature and competition were chosen because each has been long thought to be major drivers of diversity, both spatially and temporally. As Clarke succinctly put it, "temperature affects everything that an organism does" (Clarke, 2003). Above the level of the individual organism, the number of species decreases from the tropics to the poles for most taxa (Rohde, 1992): both the origin and maintenance of this latitudinal diversity gradient has been attributed in part to latitudinal temperature differences (Allen et al., 2006; Mittelbach et al., 2007). Over geological time scales, global temperatures are also proposed to control taxonomic diversity (Erwin, 2009; Mayhew et al., 2008). However, there is strong disagreement as to whether abiotic factors such as global temperature changes, or biotic factors such as competition, is the dominant determinant of biological diversity (Alroy, 2008; Benton and Emerson, 2007). While the short-term effects of biotic interactions are prominent among current day biota (Thompson, 2005), their long-term effects may be masked by dramatic abiotic change, such as those that triggered mass extinctions (Jablonski, 2008).

Our spatio-temporal model aims to describe, in an approximate way, the ecological and evolutionary responses of species to the combined effects of climate forcing and competition. We assume the earth to be a global ocean inhabited by populations of various species that survive and reproduce best at species-specific optimal temperatures. Populations reproduce, migrate, compete and undergo speciation. Local mortality results from density-dependent competition and/or a mismatch between external temperatures and biological preferences (i.e. species-specific optimal temperatures). The global extinction of any species results from the extirpation of all its component populations.

Our model is different from previous published models that generate taxon richness over geologic time scales in several important ways. It is explicitly spatial, unlike other models e.g. (Colwell and Rangel, 2010; Raup, 1985; Roberts and Newman, 1996) and the Earth's surface over which populations migrate is modelled as a sphere, as opposed to a two-dimensional plane (De Blasio and De Blasio, 2009). Our biological unit are populations, which is a natural and convenient currency of ecological and evolutionary change. Our model includes both biotic and abiotic elements, unlike models that focus on either only biotic interactions (Sevim and Rikvold, 2005) or only the abiotic environment (Colwell and Rangel, 2010). We model population mortality as a competing risk process (Prentice et al., 1978): the risk of the population failing to survive due to competition contends with that due to a mismatch between the local environmental temperature and its intrinsic temperature preference. In contrast,
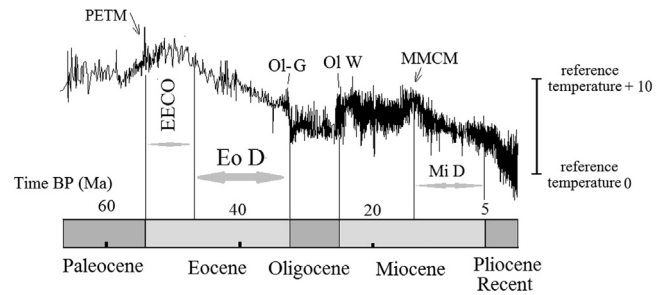

Fig. 1. Average global paleo-temperatures for the Cenozoic based on $\delta^{18}O$ (updated data from Zachos et al., 2001, pers. comm. Pagani, 2007). Climatic features discussed in our text are marked, namely the Paleocene–Eocene thermal maximum (PETM), Early Eocene Climate Optimum, (EECO), Eocene Decline in temperature (Eo D), the early Oligocene glaciation event (Ol- G), the Oligocene warming (Ol W), the Middle-Miocene thermal maximum (MMCM) and the Miocene temperature decline (Mi D).

density-dependent competition in macroevolutionary studies often consider only inter-specific competition (Phillimore and Price, 2008) although intra-specific competition is thought to be important, at least on ecological time scales (Gurevitch et al., 1992). We assume that local competition is independent of species identity, i.e. a population is equally affected by conspecific and non-conspecific populations. Last, we do not set an upper limit on the number of populations (carrying capacity).

We first study the response of the model using two simple artificial temperature time series: (i) constant temperature followed by a sudden temperature drop; (ii) periodically-changing temperatures. We then apply an empirical paleotemperature proxy (Zachos et al., 2001) to study its response over the Cenozoic, encompassing the last 65 million years (Appendix A and Fig. 1).

2. The model

We present a general model for species diversity in geological time where populations are modelled as particles that may reproduce, migrate, or become extinct. Although the model aims to be general, model parameters such as the sensitivity to temperature will depend on the properties of the organisms considered. Therefore, the specificities of the model presented are based on our understanding of marine planktic species.

Populations inhabit a spherical surface that approximates the surface oceans of the Earth. There are no continents or physical barriers to migration other than the physiological limits (temperature sensitivity) of each species. The distribution of populations and species over time and space is thus the combined result of variation in global temperature, migration of populations, speciation events, reproduction, and extinction due to environmental stress and competition both within and among species.

2.1. Numbering and characterization of species

Let us consider a certain time t when there are $N(t)$ species. A species, which is indexed with the integer j, comprises $n_j(t)$ populations indexed by $k=1,2,\ldots,n_{N(t)}$. The number of populations of a given species changes over time as new populations are born or existing ones become extinct. The total number of populations at time t is $M(t) = \Sigma_{j=1}^{N(t)} n_j(t)$.

Each species is uniquely characterized by two parameters: an optimum temperature T_j at which its populations thrive best, and a tolerance parameter σ_j for the effect on population mortality due to local temperature deviating from the species optimum. Each population is located at a point on the sphere with latitudinal and