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

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 macro-ecological 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,
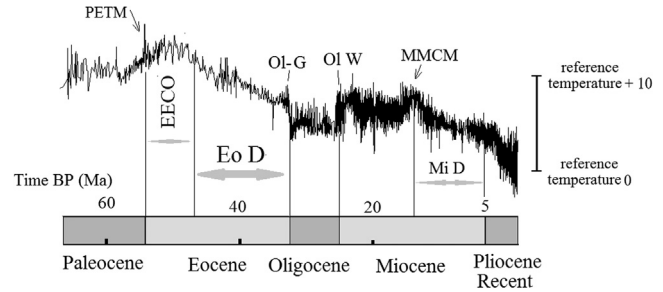

Fig. 1. Average global paleo-temperatures for the Cenozoic based on $\delta^{18}O$ (updated data from Zachos et al., 2001, pers. comm. Pagani, 2007). Climatic features discussed in our text are marked, namely the Paleocene–Eocene thermal maximum (PETM), Early Eocene Climate Optimum, (EECO), Eocene Decline 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 $k=1,2,…,n_{N(t)}$. 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

Table 1
Parameters of the model, their significance, and the values used in the calculations.

	Symbol	Name	Description	Value	Distribution
General parameters	Δt	Time step	The width of the time steps used in simulations for updates. The temporal span at which new populations and species are formed.	500–970 years	Fixed
	Ω	Maximum temperature range	Temperature difference between the equator and the poles	18 °C	Fixed
Species ecological parameters	T_j	Species optimal temperature	Temperature at which species j performs best	Stochastic	Fixed for one species until speciation takes place, where the descendent gets a new value
	σ_j	Species temperature tolerance	Range of temperature tolerated by species j, defining their adaptive span	Stochastic	Fixed for one species at 3° until speciation takes place, where the descendent gets a new value
	f	Mortality share	Divides total mortality between abiotic (environment) and biotic (competitive) risks	$0 \leq f \leq 1$; $f=0.4$ in most simulations	Fixed
	λ	Sensitivity to overcrowding	Determines how overcrowding affects extinction rate	0.01	Fixed
	γ	Payoff parameter	Regulates the advantage of being specialist versus generalist	0.1	Fixed
	Q	Payoff parameter	Regulates the advantage of being specialist versus generalist	2°	Fixed
	R	Radius of competition	Species compete only if their arc-distance is less than R	14 km	Fixed
Population generating parameters	β	Reproduction rate	Generation rate of new populations from each extant population. This is a constant for all populations.	6.5/Ma	Fixed
	σ_d	Variance of displacement distance	Variance of offspring population displacement in longitudinal and latitudinal directions relative to parent population	3°	Gaussian
Migration parameters	dm	Variance of migration distance	Migration per time step in longitudinal and latitudinal directions	0.5°	Gaussian
Species evolutionary characters	ps	Speciation probability	Proportion of population formation events that are allocated as speciation events	3% or 0.195/Ma	Fixed
	K	Maximal mortality rate	The maximum theoretical rate of a population to become extinct due to either environmental pressure of competition	28/Ma	Fixed
	$\Delta \sigma$	Change in species temperature range	Difference in adaptive width of new species relative to extant species	Average=0	Gaussian, Std=0.2, sign random
	ΔT	Change in optimal temperature	Difference in optimal temperature of new species relative to extant species	Average=0	Gaussian, Std=0.2, sign random

longitudinal coordinates (x_{jk}, y_{jk}), which can change over time due to migration. All parameters are described and specified in Table 1.

2.2. Latitudinal variation of the external temperature

The external temperature is assumed to decrease as a simple trigonometric function of latitude y

$$T(y;t) = T(0;t) - [1 - \cos y]\Omega \qquad (1)$$

where $T(0;t)$ is the temperature at the equator at time t and Ω is the temperature drop between the equator and the poles, set at 18 °C. Eq. (1) is roughly consistent with present-day equator-pole gradient temperature of shallow water, but disregards complications due to currents, bottom topography and landmasses.

2.3. Formation of new populations

At each time step, a population produces an offspring population with probability β at a location that is normally distributed around its own location, and with variance of displacement $\sigma_d^2/\cos^2(y)$ in longitudinal direction and σ_d^2 in latitudinal direction, where $\cos^2(y)$ is a distortion factor along the longitude. The directional standard deviation of displacement is set at $\sigma_d = 3°$ for our simulations. As a result, an offspring population is likely to

compete with its parental population, but since both the parent and offspring populations will migrate independently, the distance between them will tend to increase as time goes by.

2.4. Migration

During a time step, populations migrate by a jump to a new location. The displacement is independently and normally distributed in latitude and longitude, with standard deviation of displacement as d_m in both directions but with a correcting latitudinal factor $\cos(y)$. There is no explicit adaptation by migration to better temperatures; if a population migrates to favourable or unfavourable location, the consequent decrease or increase in mortality is accounted for in the 'mortality' step.

2.5. Speciation

With probability $p_s = 0.03$, a new population will belong to a different species and give rise to a speciation event. For simplicity, the new species population is located according to the same rules that apply to a new population (see Section 2.3). However, each novel species j' is assigned a new set of temperature preference parameters

$(\sigma_{j'}, T_{j'})$ based on the parameter values of (σ_j, T_j) of the parental species:

$$\sigma_{j'} = \sigma_j + \Delta\sigma \tag{2}$$

$$T_{j'} = T_j + \Delta T, \tag{3}$$

where $\Delta\sigma$, ΔT are independent and standard normally distributed, and independent of the speciation event. Because the tolerance σ_j is non-negative, the rule (2) is supplemented with a reflecting barrier at zero, $\sigma_{j'} = |\sigma_j - \Delta\sigma|$ in case when $\sigma_j + \Delta\sigma < 0$. Except for sensitivity to temperature in case by the two parameters T_j and σ_j, species are identical.

2.6. Mortality

The mortality of local populations is modelled as a competing risk process (Prentice et al., 1978) with one factor being the mismatch between local temperature and the species' optimal temperature, another being competition with other populations in the same vicinity. We discuss these in turn.

The probability for a local population to die out increases the more its optimal temperature T_j differs from the temperature experienced at its latitudinal position. Population mortality rate (in units of Ma^{-1}) due to temperature mismatch for a local population of species j located at latitude y during a given time step, is modelled as a Gaussian (e.g., Graves and Reavey, 1996)

$$m_j^{temp} = \frac{(1-f)}{(1+Q/\sigma_j)^\gamma}\left[1 - \exp\left(-\frac{2(T-T_j)^2}{\sigma_j^2}\right)\right], \tag{4}$$

where $0 \le f \le 1$ and Q, $\gamma > 0$ are payoff parameters discussed below. The mortality rate is a trough in temperature with zero mortality at $T = T_j$ with the width of the trough determined by the species-specific tolerance parameter σ_j. Functions akin to Eq. (4) have been put forward in the literature; for example, in the model of Lynch and Lande (1993) the reproduction rate (and not the mortality like here) of a population is parabolic as a function of $T - T_j$. To prevent species with high temperature tolerance from being completely resistant to temperature stress, the term $(1+Q/\sigma_j)^\gamma$ appears in the denominator. In principle, a species could benefit from a decrease of σ_j to diminish the first factor of Eq. (4), but this would only be the case at temperature close to its optimal temperature, according to Eq. (4). Species with small σ_j values are stenotopic or specialists that have high mortality outside a narrow range of temperatures. Species with high values of σ_j are eurytopic or generalists that can better withstand a temperature deviating from their temperature optimum, but which have relatively higher mortality than stenotopic ones at temperatures near their optima.

The mortality factor due to biotic competition, m^{comp}, depends on the local spatial density (within a given area of influence) of other populations. Let $f_R(x,y)$ be the number of populations located less than a great circle distance R away from the location (x,y). For a population located at (x,y) the mortality rate of death due to ecological competition during a time step is assumed to be

$$m_j^{comp} = \frac{f}{(1+Q/\sigma_j)^\gamma}\left\{1 - \exp\left[-\lambda(f_R(x,y)-1)\right]\right\} \tag{5}$$

where λ is a constant.

When $f_R(x,y) = 1$, i.e. the population at (x,y) is the only one within the critical distance, m^{comp} reduces to zero. If more populations are within the radius of competition R, then m_j^{comp} increases up to a maximum theoretical value $f/(1+Q/\sigma_j)^\gamma$. Note also that because populations inhabit the surface of a sphere, distances are not Euclidean and surface curvature must be accounted for.

With this construction, the value of the parameter f regulates the relative importance of mortality due to temperature mismatch and that due to competition. When $f = 0$ only temperature mismatch

contributes to population mortality, while when $f = 1$ only competition contributes to population mortality. Note also that inter- and intra-specific competitions are assumed to be equally stressful.

In competing risk, the various factor mortalities are stochastically independent. The probability of a local population dying during the time step Δt is thus

$$m_j = 1 - \exp\left(-K\left(m_j^{temp} + m_j^{comp}\right)\Delta t\right) \tag{6}$$

where $K > 0$ is a constant for the mortality of both temperature and competition stresses.

Note that for very small time steps Δt compared to the mortality rates, the mortality becomes approximately the sum of the two extinction agents

$$m_j \approx K\left(m_j^{temp} + m_j^{comp}\right)\Delta t \tag{7}$$

2.7. Extinction of a species

A species j is extinct when all of its populations have died out, such that $n_j = 0$.

2.8. Initialization

At the start of our simulations, 100 populations are randomly positioned on the surface of the Earth. Each of these populations represents a different species, with optimal temperature equal to the external temperature surrounding them. For a burn-in period of 200 time steps, environmental temperature is assumed temporally constant (although spatially varying as described above). Although all species are initially assigned the same temperature tolerance $\sigma \equiv \sigma_0 = 3°$, new species may be created in the burn-in period. The initial $3°$ is a conservative value relative to the median values reported from the literature for molluscs (Roy et al., 1994) and fish (Rohde and Heap, 1996).

2.9. Model scenarios

We studied the model behaviour while assuming different combinations of temperature forcing and competition. We used the following temperature forcing scenarios. (i) Temperature is constant. This simulates the response of the model subject to the only effect of competition and thus represents a check of the model response. (ii) A shift in temperature is introduced after a constant temperature, simulating a sudden environmental perturbation. (iii) The temperature perturbation is periodical. We choose sinusoidal temperature variation as it is the simplest periodical variation that also resembles natural temperature fluctuations, including Milankovitch cycles.

After testing the model with the above artificial perturbations (i–iii), we (iv) used a temperature time series based on the empirical global $\delta^{18}O$ curve as a temperature proxy (Zachos et al., 2001). The data we used is an updated version (pers. comm. Pagani 2007).

From a statistical viewpoint, our model is a complex Markov process (Pinsky and Karlin, 2011). Under constant temperature, the system will reach a stationary distribution.

2.10. Average optimal species temperature

An important feature in our model is the Average Optimal Species Temperatures (AOST) constructed as the average of all optimal physiological temperatures among the living species

$$AOST(t) = \frac{1}{M(t)}\sum_{j=1}^{N(t)} T_j(t)n_j(t). \tag{8}$$
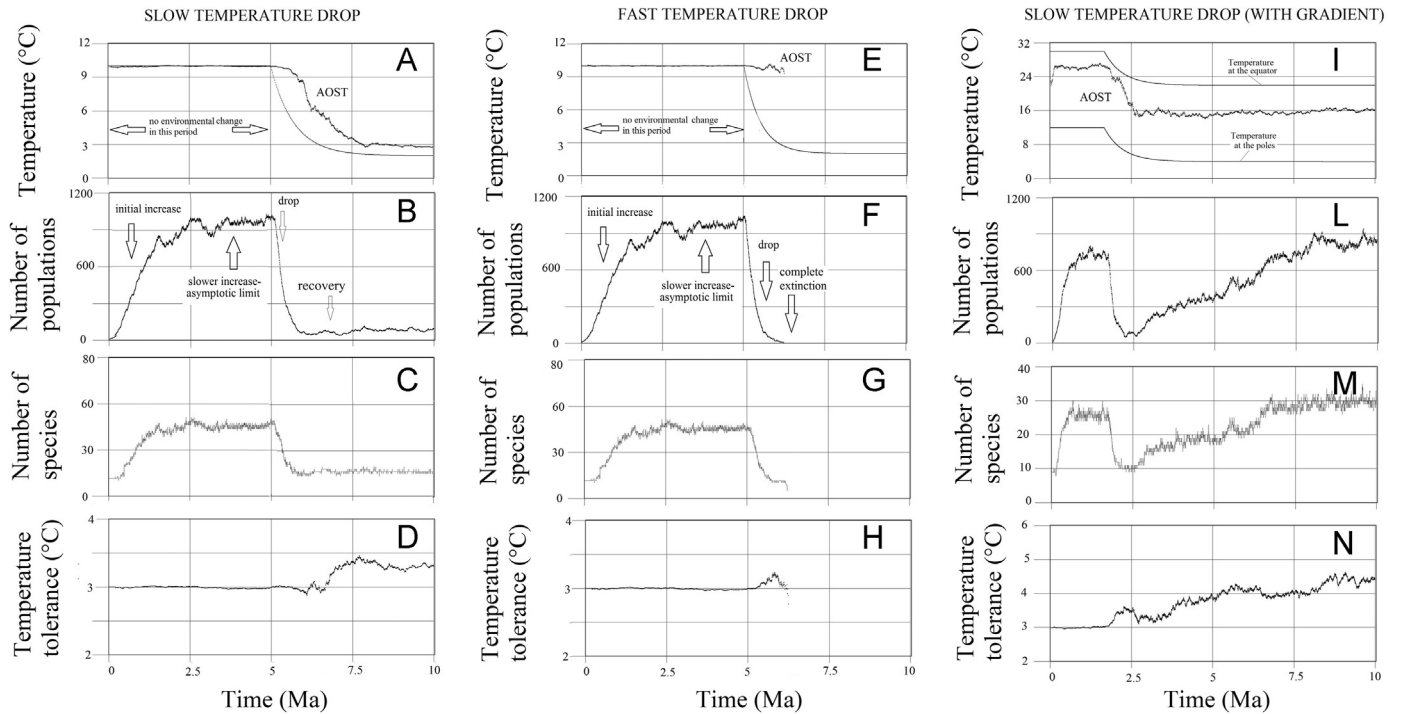
Fig. 2. Dynamics of the model with a constant temperature $T_{INITIAL}$ for the first 5 Ma followed by an exponentially decreasing temperature towards T_{FINAL}. The different panels show the external temperature and the AOST (first line), the number of populations (second line), the number of species (third line) and the average tolerance (fourth line). In the first and last columns the temperature decline was slow, while in the second column it was fast with about half the half-time. There is a latitudinal temperature gradient only in the third column, with 18° difference between the equator and the poles.

If the AOST is close to the average temperature experienced by local populations, then the environmental mortality is on average low, while it will increase as the two diverge.

3. Results

3.1. Model behaviour with artificial time series

3.1.1. Model behaviour without temperature forcing

When temperature is temporally constant, the simulated number of species and populations reach stationary distributions from arbitrary starting values (Fig. 2A–C, before 5 Ma).

3.1.2. Model response to a gradual step

After the system becomes stationary, the simplest perturbation is a temperature change from the initial value to a new limit that is approached exponentially with the time scale τ (Fig. 2). Note that there is no latitudinal temperature gradient. In the left part of the figure (Fig. 2A–D), data are shown for a relatively slow temperature change ($\tau = 1.6$ Ma). The AOST follows the temperature change with a lag as a consequence of some populations evolving to lower optimal temperatures. The number of species and population remain low for the next 5 Ma following the perturbation and it takes a long time to reach previous levels of the number of species and populations.

A fast temperature change precludes populations from adaptation by speciation (Fig. 2E–H). Rather than following the external temperature, the AOST fluctuates due to the decreasing number of populations (and thus low number of "favourable" speciation events). This ultimately leads to extinction. Interestingly, the average species tolerance (compare D and H for the two cases of slow and fast change) tends to increase in correspondence of temperature changes. This is because the temperature change prompts the selection of mutants with wider tolerance, i.e., eurytopic populations. Complete

recovery from a major extinction requires a length of time much longer than that of diversity drop (Fig. 2C and D). The explanation, as evident from our results, is that recovery requires the AOST to get much closer to the external temperature, a process that slows down as the AOST and the external temperature get closer. The dynamics of our model hence reproduces long recovery times after major extinction events (e.g., Chen and Benton, 2012), at least when abiotic gradients are absent or negligible.

Fig. 2I–N show the same perturbation as for A–D, but with a latitudinal temperature gradient with pole-equator difference of 18°. The AOST is constrained between the two temperatures at the poles and at the equator (Fig. 2I). Note that the presence of the temperature gradient ameliorates the recovery, allowing populations to reach the highest level of diversity within a relatively short time, albeit linearly, rather than exponentially. The difference between the behaviour in Fig. 2C and M is thus due to the fact that in the latter, the need for favourable speciation is bypassed by the possibility of migration.

3.1.3. Model response to sinusoidal forcing

As the global temperature varies sinusoidally with a period of 20 million years in Fig. 3A, the resulting (AOST) also varies quasi-periodically. This temporal variation is roughly sinusoidal at the same frequency as the global temperature, but the phase is slightly delayed. Population numbers and species richness are largely in phase with each other and oscillate due to the sinusoidal temperature forcing (Fig. 3B and C), while they lag slightly behind the peaks in external temperatures. Population number and species richness peaks occur when the AOST is well within the bounds of the maximum equatorial temperatures and minimum polar temperatures (the shaded area in Fig. 3A). However, in the periods in which the AOST approaches the periphery of the shaded area (around 18, 34, 41 Ma in Fig. 3), species richness and population numbers drop
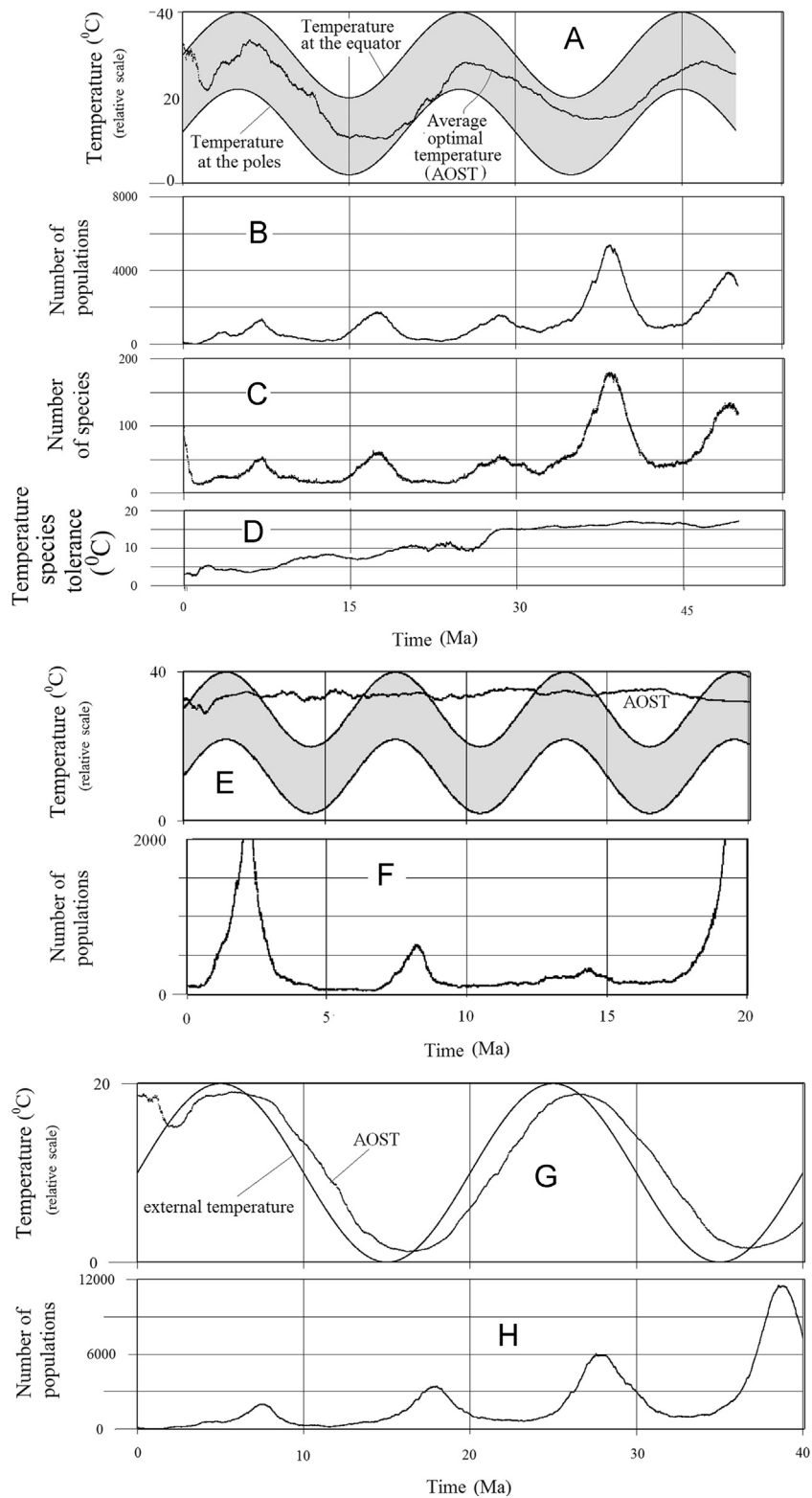
Fig. 3. Dynamics resulting from sinusoidal temperature forcing of period 20 Ma and temperature amplitude of 20°. Panel A shows the temperature forcing at the equator and poles and the Average Optimal Species Temperatures (AOST). B and C show respectively the number of populations and number of species alive, while D shows the average species temperature tolerance σ_j. Panels E and F show the results of a similar calculation with rapid variation in temperature (period of 6 Ma). Note how the average temperature preference now remains inert to external forcing. Panels G and H show the results of the simulations without latitudinal variation in temperature.

as a consequence of higher population extinction rates due to greater mismatches between external and physiological temperatures. The AOST rises with rising external temperatures, but it declines much more slowly in response to dips in external temperatures, in part because species richness is lower during these times. As a consequence of the changing environment, species tend to evolve toward greater temperature tolerance σ, thus becoming more generalist with time (Fig. 3D).

If we increase the frequency of external temperature fluctuations (period of 6 Ma) the AOST is temporally more stable (Fig. 3E). The AOST remains high as the external temperatures dip every million years or so. This is because the formation of new species (constant rate for each population) and hence generation of new values of physiological optima is not fast enough to match the external forcing. Hence, times of low temperatures also coincide with dips in species richness (Fig. 3F). As in Fig. 3B, peaks in total number of populations (Fig. 3F) correspond to the times during which the AOST is well within the bounds of the maximum equatorial temperatures and minimum polar temperatures (shaded area in Fig. 3E).

We also show the species richness and AOST curves when there is no latitudinal gradient in temperature (Fig. 3G and H). Although the model is still spatial in the sense that there is migration, the advantage of moving to a more suitable physical environment is lost. As temperature fluctuates sinusoidally but is spatially constant (Fig. 3G), the total number of populations response curve lags behind (Fig. 3H). The system has not had time to approach periodic stationarity, as it is expected to do in the long run.

3.2. Model response to empirical cenozoic temperature time series

3.2.1. Basic response of the model

Having perturbed the model with simple artificial temperature time-series, we now turn our attention to the response to global temperature changes as estimated from the geological record over the Cenozoic, i.e., over the last 65 million years (Appendix A and Fig. 1). The results of a single simulation are shown in Fig. 4. As a response to the PETM at the end of the Paleocene, the model predicts a decrease in both species richness and population numbers (Fig. 4A and B). Many species and populations become extinct due to the increased likelihood of mismatch between optimal physiological temperature and external temperature during the PETM, an equivalent of the artificial temperature shift in the temperatures of Fig. 2. Many species that survived the PETM have increased population numbers as a consequence of diminished competition. Although we do not observe any obvious changes in species or population numbers during the EECO, over the period of the declining temperature of the Eocene (Eo D) the model shows a very slow but steady increase in population numbers and species richness that persists throughout the Eocene.

At the early Oligocene glaciation (Ol-1G), species richness decreases dramatically (Fig. 4A) because model populations (Fig. 4B) do not evolve or migrate quickly enough to adapt to this rapid change. Notice how the AOST approaches the external temperatures at the equator (Fig. 4C). This implies that even in the tropics, temperatures have dropped too fast to be suitable for the existing species. In the aftermath of the Oligocene glaciation, the simulated species richness and population numbers increase and remain relatively stable for the rest of the Oligocene. The late Oligocene warming (Ol W) also produced a minor extinction.

During the Miocene, our model shows fluctuating species number and total number of populations with an overall tendency to increase throughout the Miocene. The highest species richness of the Miocene is seen close to the end of the period. Note that it does not exhibit the highest diversity during the Miocenic maximum (MMCM in Fig. 1).

The Pliocene to Holocene is characterized by rapid cooling, during which our system shows a sharp decrease in the AOST. Despite the initial generation of many new species and populations (Fig. 4A and B) during the late Miocene to early Pliocene, the rapid temperature change relative to migration and speciation rates after the early Pliocene increases population vulnerability to further changes, resulting in higher extinction rates, and reflecting broad agreement with empirical data for marine plankton (Bown

et al., 2004; Ezard et al., 2011; Schmidt et al., 2004). We emphasize that the results of running the program several times with the same input parameters but different sequence of random numbers, exhibit the same key trends as those shown in Fig. 3. Results of these different simulations and a discussion of model robustness are presented in Appendix B. A progressive change in some of the key parameters, for example the mortality rate K, produces a consistently varying result.

3.2.2. The evolution of AOST over time

The Average Optimal Species Temperature (AOST) is less volatile than the external temperature curve or the species richness curve (Fig. 4A), reflecting the temporal delay in community level evolutionary response to external forcing. Its stability is especially pronounced throughout the Palaeocene and Eocene when external temperatures have been higher and more stable, but also observed even during the PETM, a time of dramatic temperature shifts. A rapid temperature change followed by return to the initial conditions does not produce a permanent shift of the AOST, even though a turnover of species does occur due to a temporary mismatch between internal and optimal temperatures. However, when the temperature decline is more permanent, such as during the Plio-Pleistocene, species temperature optima shift permanently and this is reflected in the AOST curve (Fig. 4C).

3.2.3. The evolution of tolerance with time

Simulations start with each species having a temperature tolerance of 3 °C (Fig. 4D). However, due to selective pressures of temperature fluctuations through the Cenozoic, the average species tolerance fluctuates, as does the number of tolerant species. As a rule, a sustained period of change favours an increase in tolerance, whereas a stationary forcing is associated to a decrease of tolerance (Figs. 2 and 3). Thus, the preponderance of generalist species is a response of the community to increasing temperature fluctuations.

3.3. Model behaviour with and without competition

The suppression of the competition component of our model helps us to test whether abiotic forcing alone is sufficient to drive diversity dynamics over long-time scales (Benton, 2009; Blois and Hadly, 2009). We observe that the absence of competition greatly increases the sensitivity of our system to variation in temperature. The system becomes also highly unstable, reaching both extremely low and high species numbers. In fact, the factor K in Eq. (6) had to be tuned to prevent our simulations to reach uncontrollable values as a consequence of exponential increases in population numbers. Typically, species richness drops to very low levels during periods of rapid environmental change. On the other hand, during periods of stability, population numbers increases without bound. Fig. 5 shows a typical simulation using the empirical temperature proxy time series (as in Fig. 4), but with $f=0$ so that mortality only depends on temperature fluctuations. The system responds dramatically to the relatively small fluctuations at the beginning of the Cenozoic and increases exponentially after 7.5 million years. This result is very different from the prediction of the full model, where extinction is controlled by a combination of both temperature fluctuations and competition. How much each of these drivers contributes to extinction varies through time (Fig. 4E), and depends on parameter values. Environmental pressure is higher during periods of rapid environmental change, in particular in correspondence of the initial Oligocene glaciation (Ol-G) and the Pliocene–Pleistocene but it never reaches the maximum theoretical value of 1, implying that with the chosen parameters, extinction due to competition is always operating on the system.
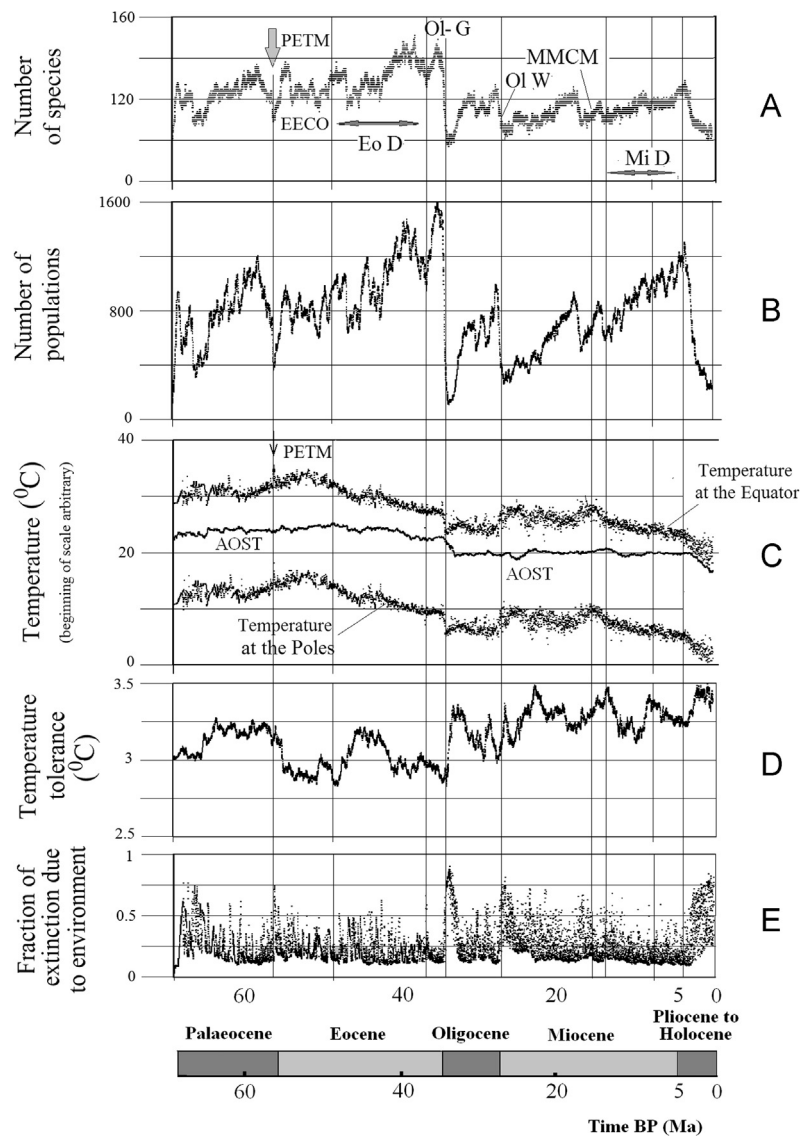
Fig. 4. Results with forcing by empirical temperature series, (A) number of species; (B) total population; (C) average optimal temperature of all the populations and for those at the poles and at the equator; (D) average species temperature tolerance; (E) the ratio $m_{env}/(m_{env}+m_{comp})$ between the average extinction rates due to the environment and the total extinction rate. A total of 67,000 time steps has been used in this simulation.
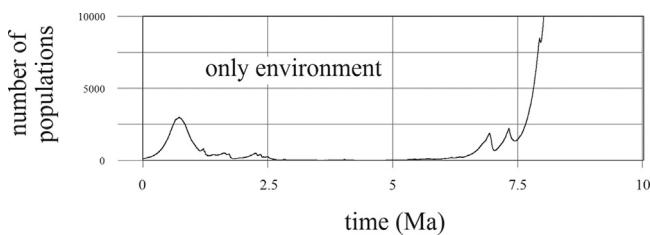

Fig. 5. Total number of populations in the absence of competition.

4. Discussion

The literature abounds with studies that examine how time series of taxonomic diversity vary with climate (Mayhew et al., 2008; Schmidt et al., 2004; van Dam et al., 2006), but generalities are difficult to extract (Erwin, 2009). This is in part because of clade specific response to climate change, and the inherent difficulties of estimating diversity where preservation probabilities are temporally and spatially heterogeneous (Kidwell and Holland, 2002; Foote, 2003; Liow and Nichols, 2010). To circumvent some of these difficulties we formulated a simple spatial model to make general observations on biotic and abiotic factors as evolutionary driving forces.

4.1. Competition as a stabilizing mechanism on long time scales

Abiotic or biotic forcing alone captures fewer features of empirical time series of taxon richness than in combination. When abiotic forcing (such as temperature fluctuations modelled here) is absent from our model, species and population turnover continue due to competition, as described in the Red Queen metaphor (Liow et al., 2011). When competition is absent, model simulations become extremely sensitive to the abiotic forcing (Fig. 5), creating patterns not observed in empirical systems. Thus, in our model, ecological competition is a stabilizing mechanism over evolutionary time scales. This observation corroborates studies that show that biotic factors may have a strong impact on long-term diversification (Alroy, 2008). In addition, a "carrying capacity" naturally emerges from the competition component in our model (see Fig. 2) in the absence of an explicitly imposed limit to population or species numbers.

4.2. Rate of temperature fluctuations

In our model the rate of temperature fluctuations has a substantial role in controlling species number and population abundance. However, temperature need not be the only driver for species distribution nor are we primarily trying to show the validity of temperature as an evolutionary driver on geological time scales. The real world is necessarily more complex where different environment factors have orthogonal, parallel or opposite effects to other factors in driving speciation and extinction. Where rates of environmental change are slower and fluctuations less volatile, species richness and population numbers tend be higher in our model, in agreement with empirical observations (Gibbs et al., 2006). Long periods with slow change in temperatures (regardless of whether they are stationary, trending up or down) are also associated with higher species diversity because of dampened extinction rates and an increase in eurytopy.

4.3. A 'memory' of abiotic changes

In our model the history of temperature fluctuations influences future diversity patterns. If a previous period has been characterized by strong fluctuations, surviving species and their descendents will tend toward eurytopy. A sudden change in subsequent temperature will thus be better tolerated by eurytopic species so that the diversity drop will not be as great. This is exemplified by the build-up of eurytopic species during the late Oligocene such that the early Miocene glaciation did not cause a substantial dip in species numbers as compared with the early Oligocene glaciation (Fig. 1). In contrast, if a sudden change in temperature occurs after a period of small fluctuations, the decrease in diversity will be dramatic, as observed during the PETM and the beginning of the Oligocene glaciation. This observation corroborates an earlier finding that species previously exposed to volatile temperatures are less prone to extinction (Liow et al., 2010). In short, the biotic system has a "memory" of previous environmental conditions.

4.4. Freely dispersing plankton on an edgeless spatial globe

Non-spatial and spatial models (De Blasio and De Blasio, 2009), and the latter with and without gradients, lead to different predictions. We have shown that species richness is high when the AOST falls within the boundaries of the maximum tropical temperature and minimum polar temperature (Fig. 2A, shaded area). This is because the bulk of the extant populations have optimal species temperatures that match well with the local temperatures, due to migration and the selective mortality. Without looking at these boundaries of extreme temperatures, one might conclude that species richness peaks when temperatures are higher (Fig. 2). But in our model, this is a clear consequence of the AOST being bounded by these external extremes. In contrast, for a model where "tropical" and "polar" temperatures are the same (Fig. 2G), populations find themselves in an optimal external temperature only when the global temperature exactly matches their internal optimum. This is highly unrealistic given that many abiotic factors that are biologically important, such as temperature and irradiation, have spatial gradients in the real world.

In the simulations we have arbitrarily chosen a value of 0.5 degrees per time step, as we are not aware of any widely accepted average migration or dispersal rates for marine plankton. In a geologically short time span of some million years, any species could have spread all over the globe, that is "everything is everywhere" (Finlay, 2002; Foissner, 2006). However, realized migration rates are a function of environmental suitability (the match of external and physiological temperatures) and density-dependent competition. It is these realized migration rates that ultimately affect the outcomes of our simulations.

4.5. Model predictions versus the real world

Our main model predictions (Fig. 4) match several common features of empirical curves of marine taxa: dips in species richness at the PETM, early Oligocene and the Plio-Pleistocene boundary are observed in calcareous nannoplankton, including coccolithophores (Bown et al., 2004) and macroperforate foraminifera (Ezard et al., 2011) (although see Rabosky and Sorhannus, 2009; Schmidt et al., 2004). The slow, but persistent predicted increase in species richness over the Eocene is observed in diatoms (Lazarus et al., 2014). Similarly, the Miocene shows an increase species richness, again observed in calcareous nannoplankton, macroperforate foraminifera and diatoms (Bown et al., 2004; Ezard et al., 2011; Schmidt et al., 2004, Lazarus et al., 2014, but see Rabosky and Sorhannus, 2009).

In addition, the decline in population numbers from the Eocene to the Oligocene, and the increasing population numbers over the Miocene is suggestive of empirical coccolithophore patterns (see Hannisdal et al., 2012).

The fact that our simulations are broadly similar to empirical data for planktic species indicates that the model contains major control factors for diversity. However, we did not attempt to statistically fit our model results to empirical time series for two reasons. First, our model is a radical simplification of the real world, hence we do not expect all of the trends and details to replicate those in the real world, which consists of clades that are very different in their biology. Moreover, diversity estimation using the fossil record is plagued with uncertainty not least due to heterogeneous preservation and biased sampling.

4.6. Eurytopic and disaster taxa

Our model predicts a slight increase in richness of eurytopic species starting from the Oligocene (Fig. 4D), a response that can be attributed to the increased variation in temperature (Fig. 1). Average tolerance increases during episodes of strong temperature forcing, and decreases when climatic conditions become more constant. However, the inclusion of multiple environmental variables beyond temperature will likely complicate patterns. A whole suite of empirical studies have shown that generalists have greater survivorship in the fossil record (Colles et al., 2009), and our model provides a likely explanation of how generalists might arise due to environmental stimulation. The same dynamics may explain why high environmental volatility early in the life of a species positively correlates with their duration in the fossil record (Liow et al., 2010).

Our model captures the typical behaviour of opportunistic and disaster taxa (Rodland and Bottjer, 2001): eurytypic taxa enjoy increased population growth rates after severe environmental perturbations. This corroborates the conventional wisdom that an empty post-extinction ecospace allows the rapid expansion of surviving species, which might have been previously marginal. In our model, this expansion due to a relaxation in density-dependent competition combined with a rapid shift in environmental conditions.

4.7. Model limitations

The general correspondence of our model predictions with empirical data is encouraging but comes with caveats. First, all species and populations are formed stochastically from the same distribution, although modulated by temperature and competition. In reality, speciation rates among clades may be trait-dependent (Sanderson and Donoghue, 1996). Moreover, speciation rates may

also increase during times of higher global temperatures (Allen et al., 2006). Second, it is unlikely that intra and interspecific competition are equivalent (Mutshinda and Woiwod, 2011). Third, we modelled the world as homogenous oceans uninterrupted by land mass. However land masses, bottom topography, ocean currents, upwellings and variation in nutrient input, all influence marine plankton community diversity and number of populations. Fourth, we assumed that latitudinal temperature variation is fixed, but latitudinal temperature gradients have not been constant over time (Utescher et al., 2011). Fifth, although we fixed a migration rate for our simulations, it could also be argued that migration is controlled by the velocity of oceanic currents, which is spatially and temporally heterogeneous. Finally, we used temperature as our sole abiotic driver, although tectonics, food supply and nutrient availability, substrate availability, ocean acidity, among a multitude of other factors surely also affect population growth and diversification (Benton, 2009; Erwin, 2009; Pagani et al., 2005; Martin, 1997; Allmon and Martin, 2014). In addition, the interplay between species fitness and other abiotic variables may involve complex biogeochemical interplay yet to be understood. From a computational viewpoint, our model can be extended to alleviate some of its current limitations, albeit at a cost of making it more complex, less tractable and interpretable. More transparency might, on the other hand, be obtained with a simpler model but at the cost of less realism and decreased possibility to investigate the interplay of environmental and biotic processes in macroevolution on our heterogeneous Earth.

5. Conclusions and future directions

Our simulated diversity curves consistently reproduced several prominent patterns observed in empirical diversity curves of plankton. This gives us some confidence that we have appropriately modelled important components of diversity dynamics observable on geological time scales. The model allows us to retrospectively better understand the controls on species diversity. For example, the drop in diversity and population abundance at the beginning of the Oligocene is caused by a rate of environmental change too high for migration and/or speciation to close the lag between external and optimal temperatures. If the late Paleocene had been environmentally more volatile, the early Oligocene crash may have been gentler, due to a "memory effect". This "memory effect" is a consequence of the model, not a specification thereof.

The model could be improved in many ways. Including more stringent migration constraints will, for example, make it applicable to benthic or terrestrial systems. Another use of the model would be to tune it to shorter ecological time scales in order to forecast changes in species richness, given different scenarios of predicted future climate changes.

Without modifications, this model allows us to explore the evolution of latitudinal ranges and individual species occurrence trajectories, which are known to vary through the lifetime of individual taxa (Foote et al., 2007; Liow et al., 2010; Liow and Stenseth, 2007).

While models like this one sacrifice complexity for tractability, they provide a tool to explore plausible mechanisms in a very complex world.

Acknowledgements

Appendix A. Cenozoic temperature changes

Here, we briefly summarize the features of the empirical temperature proxy curve and the inferred changes in global temperatures we will focus our discussions on (Fig. 1).

The Paleocene was a warm period with relatively stable temperatures, despite short-term fluctuations. The transition between the Paleocene and the Eocene, however, is marked by a short and sudden episode of strong temperature increase (PETM or Paleocene–Eocene thermal maximum) probably caused by global release of methane hydrates in the sea (Gingerich, 2006). The rest of the Eocene is characterized first by an early increase in global temperature (EECO or Early Eocene Climate Optimum), followed by a slow but constant decrease lasting for the rest of the Eocene (Eocene decrease, or Eo D). The beginning of the Oligocene is marked by a sharp decrease in the temperatures (abbreviated here as Ol- G, where "G" stands for "glaciation"); temperatures remain low until late in the Oligocene where data show a marked increase (Oligocene warming, Ol W). This is then rapidly followed by an early Miocene glaciation. This post-glaciation period sees stable temperatures for the first half of the Miocene. Around mid-Miocene, we see peak temperatures for the Miocene (MMCM or Mid-Miocene Climatic Optimum), after which there is a long-term decrease in temperatures toward the end of the Miocene (Mi D). From the Pliocene, the average temperature decreases at a faster pace (Zachos et al., 2001). Fluctuations increase in magnitude, culminating with the glacial episodes of the Pleistocene.

Appendix B. Repeatability of single calculations and model robustness

The repeatability and robustness of the model requires that: (i) calculations with different sequence of random numbers and the same input parameters should give comparable results, with randomness resulting in relatively small variations, and: (ii) when at least one of the parameters is changed from one simulation to another, results should be consistently different. Throughout numerous numerical simulations, the model has been checked for both conditions. As an example, we report here two sequences of results.

Fig. 6A shows total population numbers in replicate runs with the same input parameters as for Fig. 4, but different sequence of random numbers. For most simulations, results appear to be similar, which implies absence of dramatic dependence on random conditions.

However, for particular values of the parameters, critical behaviour can be observed in the simulations. Note the outcome if mortality rate K is increased for example from 28/Ma to 35/Ma (Fig. 6B). While some simulations reproduce results very similar to the previous case with just a lower level of population number and species richness, in some cases a crisis in population number may extinguish life. Thus, runs 5 and 6 of Fig. 6B terminate much earlier, in correspondence of the initial Oligocene crisis. The reason is that simulated crises such as the Oligocene are so dramatic that only very few populations survive. We also reported in Fig. 6 the number of populations resulting from an average over 25 runs in the two respective cases. This graph emphasizes the regions of 'genuine' changes in population number directly related to the environment, mediating over fluctuations dependent on the sequence of random numbers.

We also checked that the results obtained by progressively reducing the extinction rate from one simulation to the next lead to consistently varying results. In particular, we observed that even though the range of survival increases progressively as extinction rate is decreased, the position in time of the episodes of low diversity remains the same in all simulations, corresponding to the strong temperature changes of the Cenozoic.
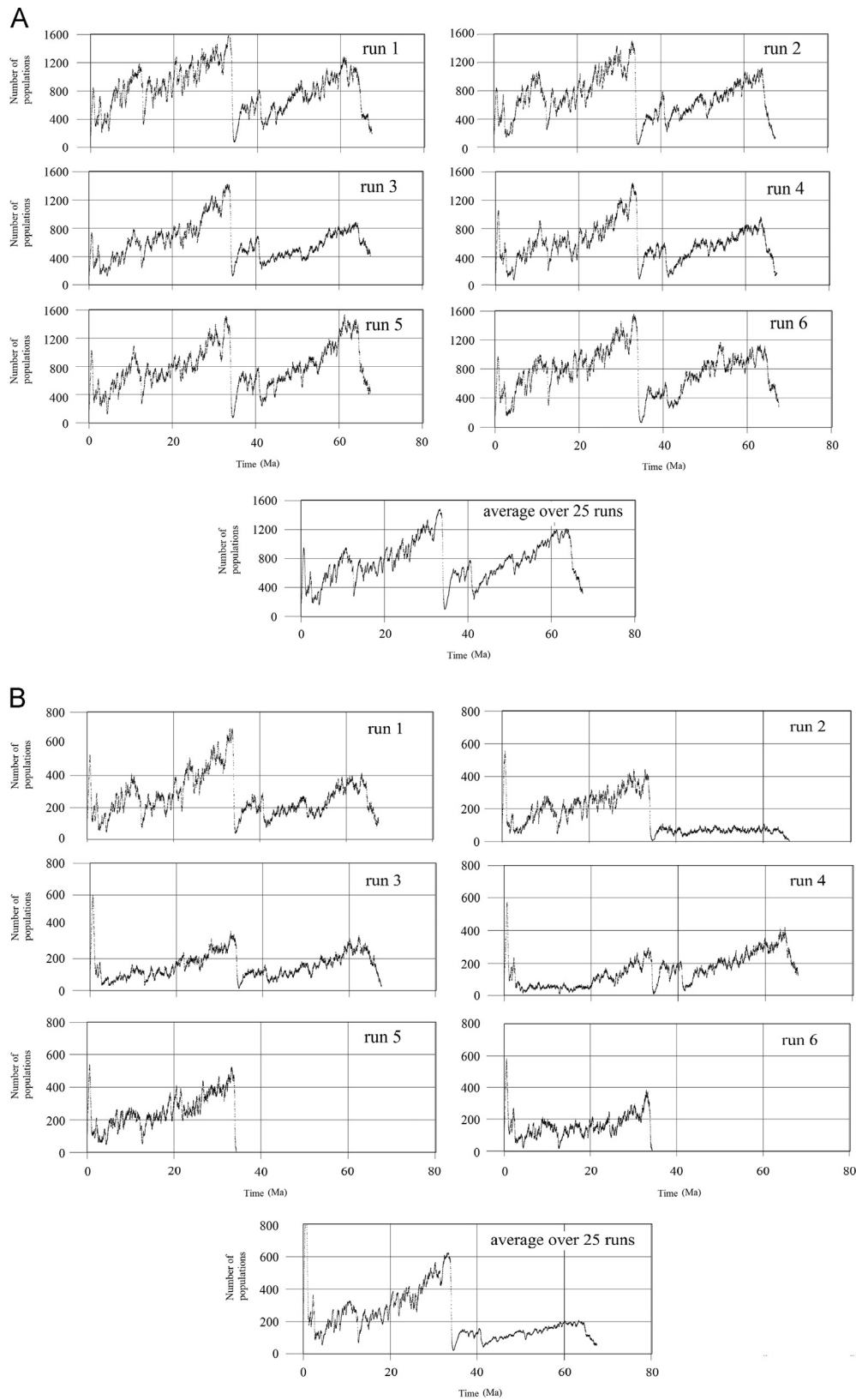
Fig. 6. Total number of populations in the first 6 replicate runs for different sequences of random numbers. (A) Simulations with input parameters identical to those used to construct Fig. 2. The last graph is an average over 25 runs. (B) The same as in A, but with the extinction rate increased to 35/Ma. Total extinction in some runs, e.g. runs 5 and 6.

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