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www.sciencemag.org/cgi/content/full/332/6027/346/DC1
Materials and Methods
SOM Text
Figs. S1 to S8
Tables S1 to S4
References

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Interplay Between Changing Climate and Species' Ecology Drives Macroevolutionary Dynamics

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Ecological change provokes speciation and extinction, but our knowledge of the interplay among the biotic and abiotic drivers of macroevolution remains limited. Using the unparalleled fossil record of Cenozoic macroperforate planktonic foraminifera, we demonstrate that macroevolutionary dynamics depend on the interaction between species' ecology and the changing climate. This interplay drives diversification but differs between speciation probability and extinction risk: Speciation was more strongly shaped by diversity dependence than by climate change, whereas the reverse was true for extinction. Crucially, no single ecology was optimal in all environments, and species with distinct ecologies had significantly different probabilities of speciation and extinction. The ensuing macroevolutionary dynamics depend fundamentally on the ecological structure of species' assemblages.

The wide-ranging mechanisms that generate and maintain biodiversity have been grouped in many different ways, but a fundamental distinction exists between biotic and abiotic drivers (*1*–*5*). If interactions among species are the dominant drivers of evolution, as in the "Red Queen" model (*1*, *4*), then diversification rates among groups of interacting species are expected to show diversity-dependent dynamics with ongoing turnover at equilibrium. A consequence of this mechanism is that diversification rates are expected to decrease as a function of diversity. Conversely, if evolution is driven chiefly by changes in the physical environment—as in the "Court Jester" model (*3*), named to contrast with the Red Queen—macroevolutionary dynamics should be dominated by cladewide effects of abrupt abiotic perturbations. Although the interplay between these alternative drivers has long been recognized as fundamental for regulating diversity (*6*, *7*), progress toward understanding their interaction has been slow (*2*). The incompleteness of the fossil record often necessitates temporally and taxonomically coarse paleontological analyses (*7*–*10*), whereas molecular phylogenies are restricted to extant species and therefore offer little insight into extinction (*11*, *12*). To distinguish how interwoven biotic and abiotic processes regulate diversity, high-resolution data on multiple forcing mechanisms should be allied to paleontological, species-level phylogenies constructed on sufficiently complete fossil records over substantial periods of evolutionary history. This resolution is rare (*2*, *6*), but Cenozoic macroperforate planktonic foraminifera provide a suitable record for testing these hypotheses (*13*).

Planktonic foraminifera are sexually reproducing protists distributed throughout the world's oceans. The calcium carbonate "shells" (known as "tests") of dead individuals rain down on the ocean floor and can, under favorable conditions, generate continuous microfossil sequences that span millions of years. The group's usefulness for stratigraphic correlation (*14*) and paleoclimatic reconstruction (*15*) has led to extensive documentation of its morphology (*14*) and depth habitats (*13*). The phylogenetic relationships within the macroperforate clade of the Cenozoic have recently been revised comprehensively (*13*), via the application of Simpson's evolutionary species concept (*16*). Under this concept, each species is intended to represent a single line of descent (*16*) that begins with a speciation (clado-

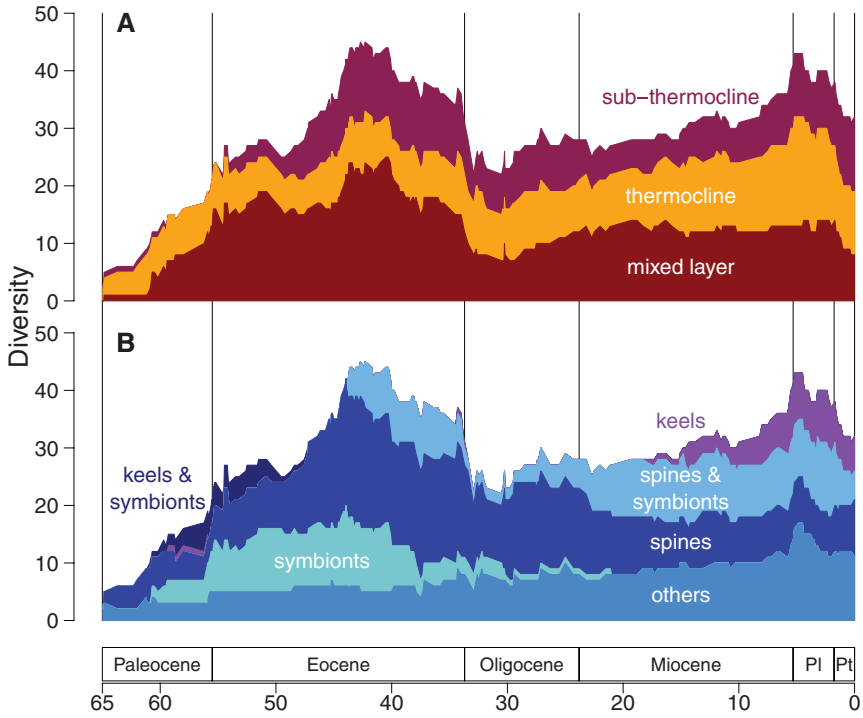

Fig. 1. The relative frequencies of depth habitats (**A**) and morphologies (**B**) of macroperforate planktonic foraminifer species across the Cenozoic (*13*) has fluctuated substantially. Time (million years before the present) is based on the marine geological time scale (*14*). Pl, Pliocene; Pt, Pleistocene.

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genetic) event and ends in extinction. The completeness of this group's fossil record is such that species have at least an 81% chance of being detected per million-year interval (fig. S2). Therefore, this species-level fossil record is at least as good as the best-preserved genus-level records of macro-invertebrates (*17*).

The macroperforate clade has diversified from two species that survived the end-Cretaceous mass extinction into 32 morphologically distinct species today, though the rise in diversity has been far from smooth (Fig. 1). The sharpest fall in diversity occurred during the Eocene-Oligocene transition, when rapid global cooling led to the development of the Antarctic ice cap (*15*). This suggests that climate change has been important in macroevolution, so we used the mean and variability of oxygen isotopic composition of deep-sea carbonates to approximate the complex, multifaceted climate system (*15*, *18*). Clade growth $[\ln\left(\frac{N_{t+1}}{N_t}\right)$, detrended, where N_t is the number of species in each 1-million-year bin $t]$ was poorly predicted by climate (Fig. 2A and table S1) (*18*). Models based on diversity-dependence used diversity only at the start of each bin and assume a constant limit to niche availability (a taxonomic analog to a demographic "carrying capacity"), but predictions were similarly poor (Fig. 2B and table S1). Thus, the clade's macroevolutionary dynamics are not well predicted by either a strictly abiotic (Fig. 2A) or a strictly biotic model (Fig. 2B).

Any clade will be composed of species with distinct ecologies. If these ecologies have conferred a macroevolutionary advantage on certain species over others, models that incorporate ecology will provide a better description of observed changes in macroevolutionary dynamics than if all species are assumed equal. To test this hypothesis, we grouped species by their depth habitat and morphology, which, taken together, we used as a proxy for species' ecology (*18*). Although it is impossible to obtain an experimental link between traits and fitness in fossils, certain traits are thought to indicate functional differences that reflect different ways of life. For example, the acquisition of spines occurred in the earliest Cenozoic and is hypothesized to indicate the transition to a carnivorous diet (*19*) and to have initiated the hosting of photosynthetic algal symbionts (*20*), whereas the evolution of a keel is thought in some instances to be associated with the invasion of new depth habitats (*21*). The assemblage in the warm Eocene oceans was dominated by species inhabiting the mixed layer, whereas most species in the stratified oceans of the Pliocene lived and reproduced near the thermocline, where the temperature gradient is much steeper than elsewhere in the water column. The ecological composition of the clade has fluctuated (Fig. 1), with the relative dominance of each group apparently waxing and waning with the changing climate.

Ecology is more strongly predictive of clade growth than either climate or diversity, but model fit is moderate at best (Fig. 2C and table S1). Models containing interactions among pairs of these variables are significantly better, but model support was strong only when species with distinct ecologies were permitted to respond differently to changes in diversity and climate (evidence weight > 0.99) (Fig. 2F and table S1). The importance of interactions among climate, diversity, and ecology suggests that ecological variation enabled the clade's standing diversity to respond rapidly to climatic fluctuations. This interpretation strengthens arguments that the Red Queen and the Court Jester are not mutually exclusive hypotheses of evolutionary diversification (*2*).

Discrete-time analysis (as is described above) may introduce bias when diversification occurs in continuous time, because there is no ideal bin length to maximize the accuracy of clade-growth estimates (*22*). Here, we use the Euler-Lotka equation (*22*, *23*) to provide an estimate of per-capita growth for an ecologically structured clade with ongoing speciation and extinction. We used parametric survival analysis with censoring (*24*) to obtain parsimonious extinction and spe-

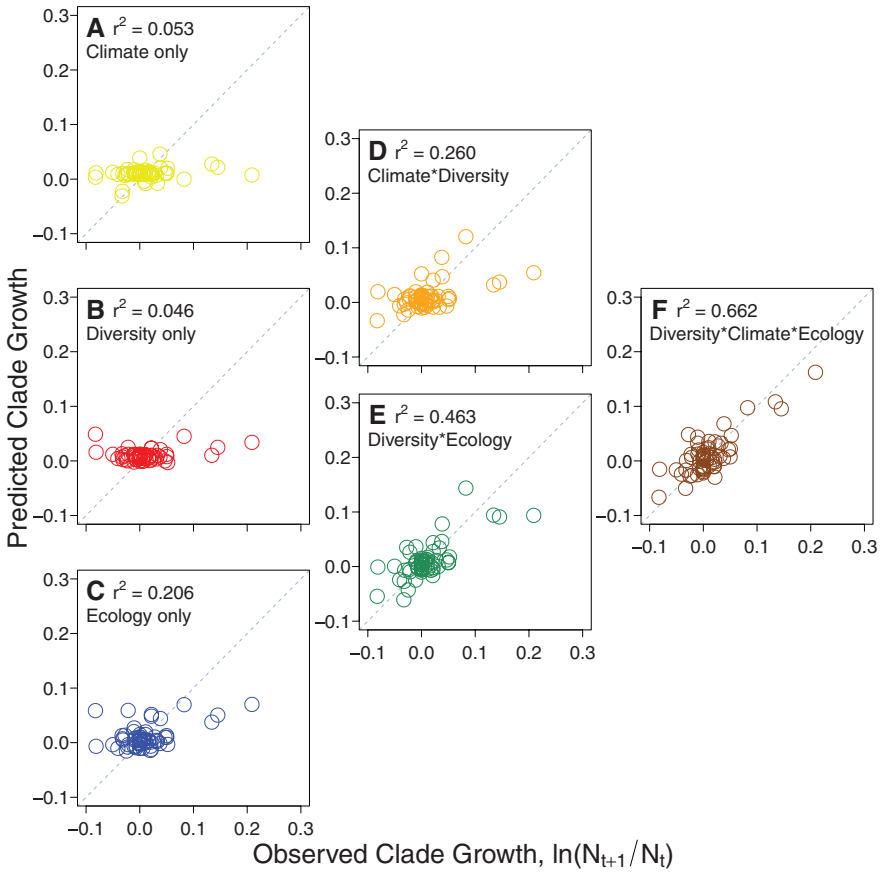

Fig. 2. (**A** to **F**) Discrete time models incorporating interactions among diversity, climate, and species' ecology outperformed all others. The dashed gray line is $y = x$; a model that predicts observed clade growth perfectly would have points only on this line. For all summary statistics and models, see table S1. r^2, fraction of total variance explained by the model.

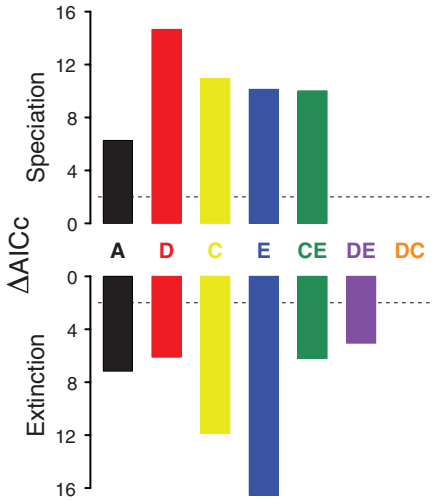

Fig. 3. Speciation probability and extinction risk varied significantly with species' age (A), diversity (D), climate (C), species' ecology (E), and their interactions (letter combinations). The dashed lines denote a difference in corrected Akaike information criterion (ΔAICc) of 2; interactions that did not reach this threshold for "substantial" support and inclusion in the model (*25*) are not shown (*18*).

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ciation functions (*18*, *25*). This approach does not resort to discretizing a continuous process and allows direct testing of two cornerstone assumptions of macroevolutionary theory (*26*): The age of a species does not influence its chances of going extinct [i.e., Van Valen's law (*1*)] or of speciating.

Extinction risk increased with age when diversity dependence, climate change, and species' ecology were incorporated. This suggests rejection of Van Valen's law [for similar patterns in morphospecies, see (*27*)], though we note that the lower extinction risk of young species may reflect a veil line in the detection probability of short-lived species over the 65-million-year-long Cenozoic era. We also found that the species most likely to speciate were young (fig. S3). This result is consistent with the frequently observed "early burst" pattern of diversification, in which rapid clade growth occurs over short periods of geological time early in a clade's history and slows thereafter due to diversity dependence (*28*). Speciation probability was affected more by biotic variables than by abiotic ones, whereas the opposite was true for extinction risk (Fig. 3). Species' ecology meant that the impacts of diversity and climatic fluctuations were not felt uniformly across the phylogeny: The extinction and speciation functions differed among species with photosymbionts, keels, and spines, and between greenhouse and icehouse oceans (fig. S3). Identifying a fixed carrying capacity is nontrivial, because the response of any assemblage to climate change depends on the species within it (fig. S4) and differs between speciation probability and extinction risk (Fig. 3). Not all species are one and the same: Ignoring their ecological differences limits understanding of the clade's macroevolutionary dynamics.

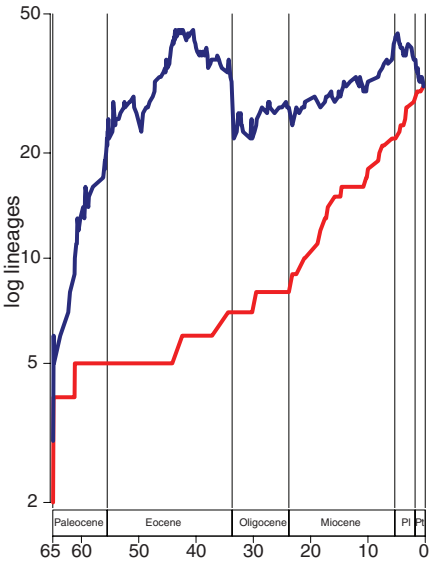

Fig. 4. The impact of extinction on macroevolutionary dynamics of macroperforate planktonic foraminifera is clear when fossil species are used (blue), but not when analysis is based solely on extant lineages (red). Time (million years before the present) is based on the marine geological time scale (*14*).

The continuous-time model gives a deterministic measure of clade growth. We incorporated the impact of changing diversity and climate by parameterizing these variables at speciation and thus assume that conditions early in a species' existence have long-lasting evolutionary consequences. Taking an approach that spans the Cenozoic maximizes the number of bursts of diversification under investigation but restricts our ability to disentangle complex components of climate change and how they affect biodiversity. Despite these limiting assumptions, the continuous-time model captured key features of the macroevolutionary dynamics, such as highest clade growth in greenhouse and highly stratified oceans (fig. S4). The binned analysis is complementary to the continuous-time analysis because it incorporates climate variability during a species' existence (though still assumes a single proxy for climate). The consistency of conclusions from the two approaches supports our interpretation that diversity dependence, climate change, and species' ecology interact to drive macroevolutionary dynamics. Approaches based only on extant diversity can identify some components of diversification (table S4), but they neglect competition among now-extinct species and therefore cannot reveal how biotic interactions among them affected diversity patterns in past environments (Fig. 4).

What biotic and abiotic factors should models of diversification consider? An often-invoked null hypothesis is constancy of birth and death rates; for instance, the constant-rates Markov model (*26*). The ubiquitous importance of species-level diversity dependence in the models presented here violates this fundamental assumption. The less restrictive, equal-rates Markov model permits speciation and extinction probabilities to change through time, provided that they do not vary among contemporaneous species (*26*). This assumption is opposed by our result that young species with similar ecologies are more likely to speciate under particular climatic conditions than older species with other ecologies (Fig. 3 and fig. S4). Finally, speciation probability was more strongly shaped by diversity dependence than by climate change, whereas the reverse was true for extinction risk (Fig. 3). Decomposing macroevolutionary dynamics into its constituent parts is a useful step toward a more complete understanding of how biodiversity is generated and destroyed (*8*).

We conclude that neither the Red Queen nor the Court Jester hypothesis is the dominant macroevolutionary force; instead, it is the interplay of biotic and abiotic variables that regulates diversity and drives speciation and extinction (Figs. 2 and 3). Contrary to recent analyses of global marine diversity patterns (*9*), our results suggest that species' ecology plays a key role in determining overall diversity and gives clearer insights into macroevolutionary dynamics than is possible by treating clades as homogeneous wholes.

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Supporting Online Material

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Materials and Methods
Figs. S1 to S4
Tables S1 to S4
References and Notes

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