



SYMPOSIUM

Loss of Biodiversity Dimensions through Shifting Climates and Ancient Mass Extinctions

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Synopsis Many aspects of climate affect the deployment of biodiversity in time and space, and so changes in climate might be expected to drive regional and global extinction of both taxa and their ecological functions. Here we examine the association of past climate changes with extinction in marine bivalves, which are increasingly used as a model system for macroecological and macroevolutionary analysis. Focusing on the Cenozoic Era (66 Myr ago to the present), we analyze extinction patterns in shallow-water marine bivalve genera relative to temperature dynamics as estimated from isotopic data in microfossils. When the entire Cenozoic timeseries is considered, extinction intensity is not significantly associated with the mean temperature or the detrended variance in temperature within a given time interval (stratigraphic stage). However, extinction increases significantly with both the rate of temperature change within the stage of extinction and the absolute change in mean temperature from the preceding stage to the stage of extinction. Thus, several extinction events, particularly the extinction pulse near the Pliocene–Pleistocene boundary, do appear to have climatic drivers. Further, the latitudinal diversity gradient today and the Cenozoic history of polar faunas suggest that long-term, regional extinctions associated with cooling removed not just taxa but a variety of ecological functions from high-latitude seas. These dynamics of biodiversity loss contrast with the two mass extinctions bracketing the Mesozoic Era, which had negligible effects on the diversity of ecological functions despite removing nearly as many taxa as the latitudinal gradient does today. Thus, the fossil record raises a key issue: whether the biotic consequences of present-day stresses will more closely resemble the long-term effects of past climate changes or those that cascaded from the mass extinctions.

Introduction

Extinction varies, both spatially and temporally, in its tempo, intensity, and selectivity (Foote 2010; Orzechowski et al. 2015; Jablonski 2008, 2017). The seemingly infinite combinations implied by that observation might imply that biodiversity loss is essentially idiosyncratic, but certain extinction drivers apparently persist across extinctions fast to slow, mass to mild, and regional to global. Identifying the common mechanisms of lineage loss across seemingly disparate modes has fueled an extensive literature on the biotic and abiotic factors driving extinction. This ongoing research has discovered new fossil lineages,

improved taxonomic resolution, and refined paleoenvironmental and paleoclimatic records—all of which has significantly expanded the spatial and temporal image of extinction dynamics and the factors that underlie them. Continued investigation into these extinction drivers is needed to understand extinction’s role in shaping the modern biota and to reliably predict the nature of future biodiversity loss due to anthropogenic impacts (Harnik et al. 2012).

Here we address some of the many potential linkages between climate change and biological extinction by connecting temporal (paleontological) and spatial (present-day) patterns of taxonomic and

functional diversity. We first explore the impact of shifting temperatures on the extinction of marine bivalve genera over the past 66 Myr. We then discuss the role of climate in shaping the most pervasive present-day diversity pattern, the latitudinal diversity gradient, particularly with respect to its impact on the ecological variety of marine bivalves. We close with a discussion on how the nature of biodiversity loss through two of the largest marine mass extinctions (the end-Permian and end-Cretaceous) contrasts with expectations from the latitudinal pattern and may inform the threat to today's biodiversity in light of ongoing climatic and environmental change.

Taxonomic dimension: climate dynamics and extinction

Many climatic factors influence the accommodation of taxa on the planet today (Hillebrand 2004; Mittelbach et al. 2007) and have often been implicated in regional or global diversity dynamics in the geologic past (Erwin 2009; Crame et al. 2018). Examples range from glaciation-related marine extinctions near the end of the Ordovician (Finnegan et al. 2012) to turnover of terrestrial fauna near the Eocene–Oligocene boundary (Sun et al. 2014), but a general, continuous role for climate change in extinction remains an area of active research (Ezard et al. 2011; Mayhew et al. 2012; Norris et al. 2013; Liow et al. 2015).

Biotic responses to climatic variation through time and across space are usually analyzed in terms of temperature and its dynamics (Belanger et al. 2012; Valentine and Jablonski 2015). On a global scale, warm stable climates are associated with high global mean temperatures, coinciding with times of broad tropical extent (Estes and Hutchison 1980; Sluijs et al. 2006; Evans et al. 2018)—a climate state associated with higher taxonomic richness (Brown 2014; Fine 2015; Valentine and Jablonski 2015). Conversely, low mean temperatures tend to correspond to times of broader polar and temperate climate zones, which are associated with lower standing diversity today. Thus, shifts between mean temperature states, especially from warm to cool, may intensify extinction as latitudinal breadth of the tropical climate zone expands and contracts. The rate at which global mean temperature changes, and thus the rate at which climatic boundaries shift across latitude, could affect extinction levels to a greater degree than absolute change in temperature state itself. Relatively faster rates of temperature change could elevate the extinction risk of climatically

sensitive faunas located near major climatic boundaries in particular. Additionally, unstable climate states with high frequency fluctuations in global mean temperature on geological timescales (kyr to Myr) may elevate extinction relative to more stable periods (Fortelius et al. 2015). Accordingly, we would expect periods of directional, relatively rapid, and/or unstable climate change to increase extinction intensity.

An evolutionary laboratory: the Cenozoic bivalve fossil record

The taxonomically rich and densely sampled Cenozoic record of marine bivalves is a good macroevolutionary and macroecological laboratory for evaluating the role of climate in extinction (Crame 2000; Belanger et al. 2012; Tomašových et al. 2015). In this and other papers, we use a dataset—derived from an extensive update to Sepkoski's (2002) genus-level Phanerozoic compendium—containing the first and last stratigraphic appearances of 518 genera that went extinct during the Cenozoic and the first appearances of 1057 extant genera with a fossil record (Supplementary Dataset S1). First and last appearances of genera are classified by their occurrence in discrete time bins (formally geological stages or substages hereafter termed “stage” for brevity) using the timescale of Gradstein et al. (2012) (Supplementary Table S1). Here, we focus exclusively on bivalves that occur along the continental shelf (0–200 m water depth) because deep-sea bivalves constitute a distinct evolutionary and biogeographic assemblage (Rex and Etter 2010; Valentine and Jablonski 2015). Overall, the Cenozoic record of shelf-depth marine bivalve genera captures the major features of species-level extinction dynamics (Roy et al. 2009), is relatively robust to sampling biases with remaining preservational biases fairly well understood, and exhibits a trivial “Pull of the Recent” effect (Jablonski et al. 2003; Valentine et al. 2006). To further reduce sampling effects, we quantified the intensity of global marine bivalve extinction using per-capita values after Foote (2000): “per-capita extinction” $q = -\ln(N_{bt}/N_b)$, where N_b is the number of genera crossing the base of a stage (i.e., the oldest boundary), N_t is the number of genera crossing the top of a stage (i.e., the youngest boundary), and N_{bt} is the number of genera crossing both the base and top stage boundaries.

Variation in the duration of geological stages might influence the observed variation in extinction across the Cenozoic (Foote 2000, 2003). Stage durations peak in the early Eocene (4.1 Myr in the Early

and Late Ypresian) and decline to ~ 1 Myr in the Pliocene and Pleistocene stages (Supplementary Fig. S2A). This general decline in stage duration toward the present-day does not correlate with the magnitude of extinction (Supplementary Fig. S2B), indicating that extinction did not occur randomly or constantly through time within stages. Instead, extinction was likely concentrated toward the end of stages because geological stages are usually bounded by extinction events (Foote 2003). The independence of extinction intensity and stage duration found here provides a temporal framework for analyzing the potential effect of temperature dynamics on the extinction of marine bivalve genera through the Cenozoic.

Despite the steady increase in standing diversity through the Cenozoic, extinction varied in its timing and intensity (Fig. 1), with no apparent difference in magnitude between the Paleogene and the Neogene (Mann–Whitney $U = 126$, $P = 0.17$). Extinction also shows no relation to its value in prior stages (i.e., extinction has no temporal autocorrelation—see Supplementary Fig. S3). This qualitative mismatch between extinction levels across high and low levels of standing diversity suggests a limited effect of diversity-dependence on extinction. Thus, additional factors including climate change may better explain the variation in marine bivalve extinction through the Cenozoic.

The geological record of Cenozoic marine climate

The global history of Cenozoic climate derived from the oxygen isotope record (δO^{18}) in deep-water benthic foraminifera provides useful insight into the large-scale (Myr) temperature dynamics over the past 66 Myr (Zachos et al. 2001, 2008). The deep-sea climate record primarily reflects the minimum global temperature—i.e., the temperature of polar waters that fuel deep-ocean circulation—and thus the steepness of latitudinal thermal gradients in surface waters (Alroy et al. 2000; Zachos et al. 2001). This record captures smoothed trends in ocean climate and is commonly used for studying biological responses to climate change over geological time-scales (e.g., Ezard et al. 2011; Norris et al. 2013).

Variation in the Paleogene record of oxygen isotopes primarily reflects variation in temperature owing to low to non-existent ice volume whereas Neogene oxygen isotope values simultaneously reflect variations in temperature and ice volume (Zachos et al. 2001, 2008). Here we use an integrated temperature series of Cramer et al. (2011), which estimated deep-sea temperature by combining the

oxygen isotope record with a stratigraphic history of sea-level to account for ice volume effects in the Neogene. We rescaled temperature series to the 2012 Geological Time Scale (Gradstein et al. 2012) (Supplementary Fig. S1).

The discrete nature of the biological data (i.e., per-stage estimates of origination, extinction, and diversity) requires coarsening of the higher resolution temperature time series before testing for any potential relationships between the two. Thus, we characterized the climate state within each Cenozoic stage in three ways: (1) the mean temperature value, (2) the rate of temperature change, and (3) the degree of temperature variability (Supplementary Table S1). The rate of temperature change is the absolute value of the slope from a linear regression fit to temperature as a function of time within a stage. The detrended variance of temperature values (hereafter “detrended variance”) is the variance of the residuals from the same linear regression and accounts for the variation in temperature aside from the first-order linear trend. The summarized mean temperature reflects the general trajectory of Cenozoic temperatures well, and both the rates of temperature change within stages and the detrended variance fluctuated considerably (Fig. 1). Of the temperature summaries, only the mean series shows significant autocorrelation (Supplementary Fig. S3) that could mask the true nature of its correlation with extinction—a factor that we note in our subsequent consideration of the correlation between temperature and extinction dynamics. Overall, the three temperature summaries are not correlated with each other, and as such can be treated as independent predictors of extinction (Supplementary Fig. S4A).

Correlating extinction and climate dynamics

Correlating paleontological time series remains a pressing problem in evolutionary biology (Liow et al. 2015; Reitan and Liow 2017; Foote et al. 2018; Hannisdal and Liow 2018). Variations in the durations of measured time intervals and discrepancies on the time scales of measurements themselves violate the fundamental assumptions of common time series methods (Reitan and Liow 2017). However, the bivalve extinction data analyzed here do not show temporal autocorrelation and are uncorrelated with differences in stage duration (see above and Supplementary Fig. S2B), so we take a simple, linear approach to estimating its relationship with temperature dynamics for three scenarios:

- (1) Stage-level correlations: $q_t = T_{\mu_t} + T_r + T_{\sigma_t}$, where for stage t , q_t is the per-capita extinction

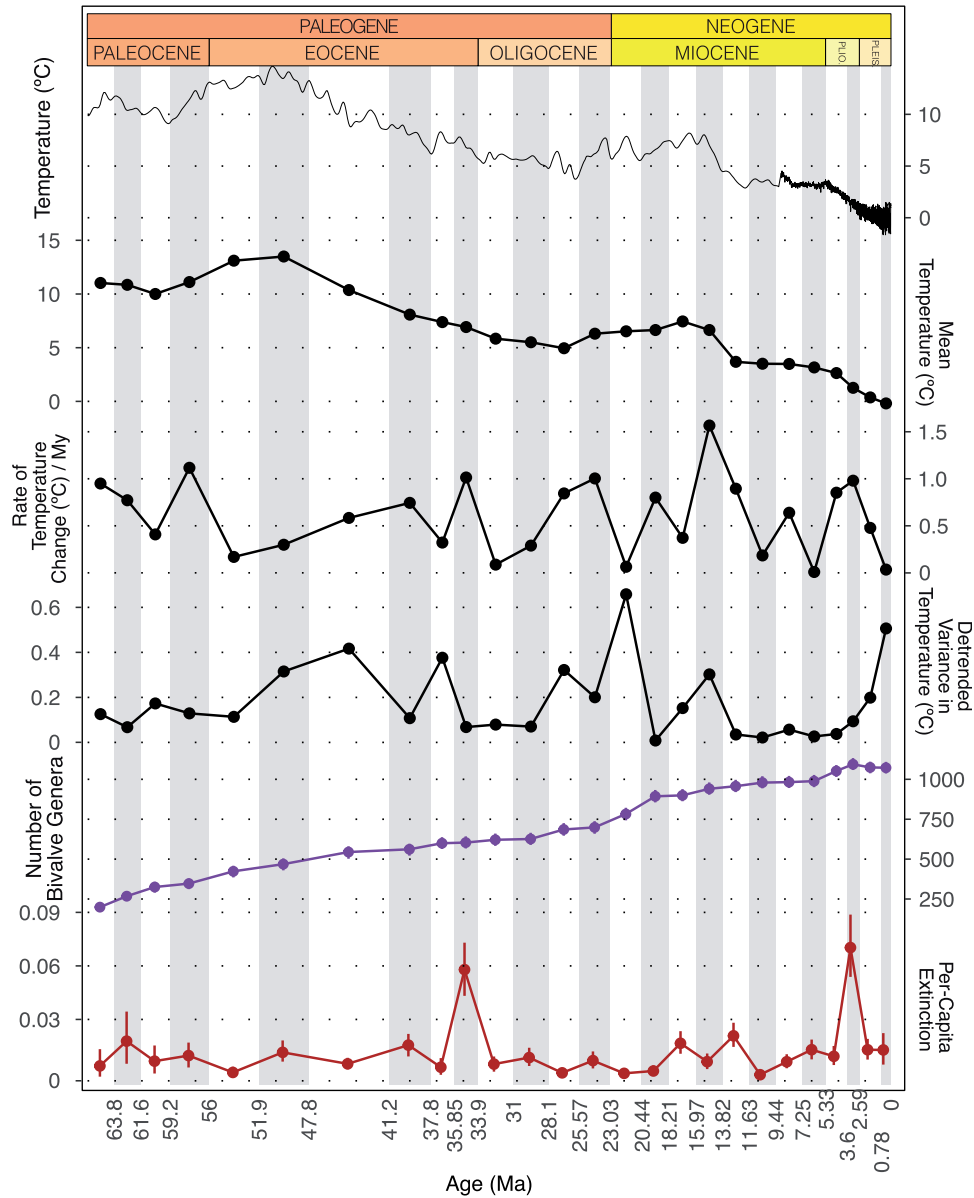


Fig. 1 Trends in climatic and biological data through the Cenozoic. Global deep-sea temperature generally declined, with the largest changes occurring through the late Paleogene and late Neogene (series from [Cramer et al. 2011](#)). The rate of temperature change within stages varied considerably with no clear directional trend through time. The detrended temperature variance within stages fluctuated through the majority of the Cenozoic and underwent a considerable increase from the Pliocene to today corresponding to high-frequency episodes of Northern Hemisphere glaciation. Diversity increased in an almost monotonic fashion, expanding from 184 genera in the early Danian to at least 1051 genera with a fossil record today. *Per capita* extinction varied through the Cenozoic and underwent notable pulsed episodes in the end-Eocene, mid-Miocene, and Plio-Pleistocene intervals.

estimated above, T_{μ_t} is the mean temperature, T_{r_t} is the absolute value of the linear rate of change in temperature, and T_{σ_t} is the detrended variance in temperature. We assumed that the summarized temperature dynamics contributed to the extinction of lineages at any point within that stage, though we expected extinctions to have largely occurred toward the later portion of the stage as discussed above.

- (2) Correlations with a one-stage lag: $q_t = T_{\mu_{t-1}} + T_{r_{t-1}} + T_{\sigma_{t-1}}$. This one-stage lag model would be biologically appropriate if extinctions are concentrated near the base of a stage, where temperature dynamics in the previous stage are more likely to have affected lineage turnover.
- (3) Correlations with first-differences in mean temperature and the within-stage rate of

temperature change: $q_t = |T_{\mu_t} - T_{\mu_{t-1}}| + T_{r_t}$. Here, two modes of temperature change could have affected extinction: first, the magnitude of change in mean temperature from the preceding stage, and second, the rate of temperature change within the stage of extinction. The change in mean temperature from the preceding stage to the stage of extinction is uncorrelated with the rate of temperature change within the stage of extinction (Pearson's $r = 0.09$, $P = 0.67$), indicating that large absolute changes in temperature do not necessarily correspond to high rates of temperature change either within the stage of extinction or before it.

Each of these models represents a plausible relationship between global temperature dynamics and extinction as outlined above. We assumed that each temperature dynamic impacted extinction and therefore evaluated their relative effects in a Bayesian framework by placing strong zero-value priors on the scale of the z-transformed predictors. All linear regressions were fit with a lognormal response distribution and predictors were given Cauchy priors with location=0 and scale=0.1 using the “brms” package in R (Bürkner 2017). In all models, the four sampling chains, each 2000 iterations long, converged to provide a stable posterior distribution of parameter estimates ($\hat{R} = 1$; Stan Development Team 2018).

Evaluating the statistical support for each model type in a model comparison framework validates our use of the fully parameterized models. Nested parameterizations of each model type were fit to the data with the same priors as specified above and then compared with each other using leave-one-out cross-validation (LOOic, Vehtari et al. 2017). For each model type, the LOOic of the fully parameterized model was within the standard error of the best supported model (Supplementary Table S2), which supports our assumption that each temperature dynamic had a measurable effect on extinction. Thus, the fully parameterized models with strong zero-value priors were used to assess the relative effects of temperature dynamics on extinction.

Shifting Cenozoic climates and taxonomic extinction in marine bivalves

Temperature dynamics play a complex role in the extinction of marine bivalves over the past 66 Myr. Greater variation in temperature within a stage as measured by the detrended variance does not

correspond to higher levels of extinction (Fig. 2C and Table 1), which is somewhat surprising given the relationship between the effect of seasonality on diversity accommodation today (Valentine 1971; Hawkins et al. 2003; Fine 2015; Valentine and Jablonski 2015). The stage-level relationship between mean temperature and extinction also shows little correlation (Fig. 2A and Table 1). Increases in the rate of temperature change within stages, however, tend to correspond with increases in extinction intensity (Fig. 2B and Table 1). A one-stage lag in temperature predictors shows a diminished effect of the rate of change in temperature, and the effect of detrended variance remains low (Fig. 2E, F and Table 1). Mean temperature in the preceding stage positively correlates with extinction (Fig. 2D and Table 1), which may actually reflect the change in temperature from the preceding stage to the stage of extinction given the general trend of cooling through the Cenozoic and the autocorrelation of the mean temperature time series.

Indeed, higher levels of extinction correspond to both larger absolute changes in mean temperature from the preceding stage to the stage of extinction and larger rates of temperature change within the stage of extinction (Fig. 2G, H and Table 1). These dynamics in temperature may have reflected the absolute shift in latitudinal position of major climate boundaries and the pace at which those shifts occurred, which could have placed temperature-related stress on faunas occurring at or near those boundaries (Roy 2001). Finer-scale consideration of regional extinction intensities can provide the necessary context to examine this potential link between shifts in climate boundaries and extinction (e.g., Jablonski et al. 2017); however, global bivalve extinction through the Cenozoic is low and the sample sizes necessary for rigorous comparisons may be difficult to achieve with the current knowledge of the stratigraphic record. It is also important to note that temperature mostly cools across Cenozoic stages, which limits our interpretation of expected extinction under current trajectories of warming today. However, the observation that extinction intensity tended to increase with larger changes in mean temperature and faster rates of change suggests that a more general link exists between temperature change and extinction irrespective of sign.

None of the models analyzed here explain more than 30% of the observed variance in extinction intensity through the Cenozoic (Table 1). The remaining variance probably derives from the many additional factors that perturb standing diversity, a number of which are only indirectly or distantly

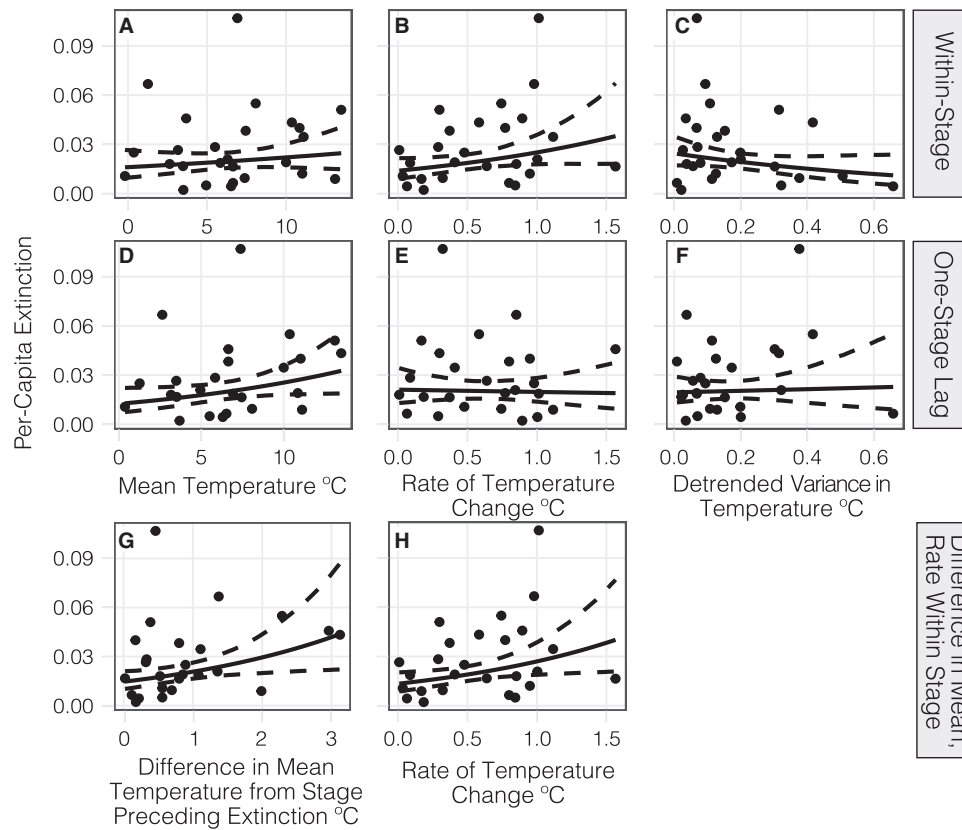


Fig. 2 Extinction of marine bivalve genera as a function of temperature dynamics. **A-C**) Partial fits of extinction as a function of additive temperature dynamics within geological stages. **D-F**) Partial fits of extinction as a function of one-stage lagged additive temperature dynamics. **G-H**) Partial fits of extinction as a function of the difference in mean temperature from the preceding stage and the rate of temperature change within a stage. Points are values for individual stages, and the solid black line represents the partial fit of the predictor to the data (i.e., the effect of the target predictor with all other predictors evaluated at their means). Dashed black lines show the 95% credible interval estimated from the model posterior. Estimated values for regression coefficients given in [Table 1](#).

Table 1 Fitted coefficients for models of extinction and temperature dynamics

	Predictor	Estimate	Pr > 0 (%)	Pr < 0 (%)	R ²
Within-stage	Mean	0.03	74	26	0.19
	Rate	0.50	88	12	
	Detrended variance	-0.66	22	78	
One-stage Lag	Mean	0.07	90	10	0.21
	Rate	-0.06	45	55	
	Detrended variance	0.12	55	45	
Difference in Mean, Within-stage Rate	Difference in Mean	0.33	95	5	0.29
	Rate	0.53	91	9	

Right-most column gives the probability that the estimated value is greater than zero.

related to the temperature values incorporated here. Changing sea-levels, nutrient regimes, oceanic oxygen, and pH levels at global and regional scales, and perhaps even the introduction of predators, parasites, and competitors, each could have contributed to extinction in marine bivalves. Of those factors, spatial

and temporal dynamics in nutrient availability and thus productivity could have a profound effect on bivalve extinction because a majority of bivalve lineages filter feed on phytoplankton ([Berke et al. 2014](#); [Edie et al. 2018](#)). However, temperature and its dynamics are a poor spatial predictor of productivity

levels today (Valentine 2009; Valentine and Jablonski 2015), which would explain the weak prediction of extinction by temperature if bivalve turnover primarily responds to changes in productivity.

A general, but weak, Cenozoic-wide signal in extinction from temperature dynamics does not exclude a larger role for temperature in other groups and at other scales. For example, climate change significantly affected extinction rates of other marine ectotherms through the Cenozoic (e.g., Ezard et al. 2011; Mayhew et al. 2012; Norris et al. 2013), and regional extinction intensities of marine bivalves across the Pliocene–Pleistocene boundary are significantly related to changes in mean annual sea-surface temperature (Jablonski et al. 2017). Although *in situ* physiological evolution in response to climate change seems feasible for marine ectotherms, the most common response has been geographic range shifts and extinctions (e.g., Valentine and Jablonski 1993; Greenstein and Pandolfi 2008). At high latitudes, diversity of fish, gastropods, and decapod crustaceans declined with polar refrigeration rather than persisting via *in situ* adaptation (Eastman 2005; Thatje et al. 2005; Krug et al. 2010; Near et al. 2012; Crame 2018). These taxonomic losses extended beyond the species level to both genera and families, thereby removing significant portions of phylogenetic diversity (e.g., Krug et al. 2010). Thus, while the Cenozoic as a whole does not show a strong climate–extinction association for marine bivalves, the biotic history of specific clades, intervals, and regions clearly indicates a role for climate in shorter-term diversity dynamics and almost certainly contributed to shaping today’s latitudinal diversity gradient.

Functional dimension: the loss of ecological variety in space and time

Climate and the structure of today’s spatial gradient in functional diversity

Biodiversity consists of more than just taxon numbers. Today, ecological and phenotypic variety generally decline toward the poles, although the details of this trend remain poorly known in most groups (see Kissling et al. [2012] for birds, Oliveira et al. [2016] for mammals, and Edie et al. [2018] for marine bivalves). The global taxonomic diversity of living marine bivalve species and genera declines by nearly an order of magnitude from the equator to poles, falling by as much as 98% at the species level from the tropical Indo-West Pacific to the Antarctic Ocean (Fig. 3C). Although many environmental and ecological factors have been hypothesized for driving

the development of this gradient in marine bivalves and other biotic systems (Mittelbach et al. 2007; Fine 2015), nearly all authors suggest that this trend is at least partly driven by one or more aspects of climate, often implicating latitudinal differences in temperature and its stability at various time scales (Brown 2014; Fine 2015; Valentine and Jablonski 2015). For marine bivalves, species richness declines with declining mean annual temperatures (Fig. 3A, C). Functional richness—the number of discrete groups of ecological function described in Supplementary Table S3—begins to decline as seasonality increases. All 49 functional groups are found in the tropics, but only 19 and 16 groups persist into the Arctic and Antarctic faunas, respectively (Fig. 3B, D).

Past climate change appears to have been important in shaping the present-day spatial gradient in functional diversity. As noted above, extinction within the Antarctic fauna through cooling, the development of the circum-Antarctic current, and alteration of habitats by sea ice near the Eocene–Oligocene boundary (Crame 2018; Crame et al. 2018) removed entire families and functional groups of bivalves that have remained absent from the fauna since that time (Krug et al. 2010). The time-integrated effects of this non-monotonic but ultimately directional trend in climate has contributed to the parallel spatial gradients in present-day taxonomic and functional richness of marine bivalves (Jablonski et al. 2017; Edie et al. 2018). Finer-scale investigation into the regional nature of other large, putatively climate-driven extinctions such as the end-Eocene would be particularly useful for determining whether climate-driven extinctions tend to be differentially concentrated within high-latitude climate zones. Further, today’s climate-driven gradient in functional and taxonomic diversity may be particularly steep relative to other times in Earth history given the always warm tropics and the currently refrigerated poles (e.g., Valentine et al. 1978). The interaction of that strong gradient with the accelerating impact of global non-climatic factors may exacerbate current pressures—a potential interaction of current pressures with today’s biogeographic configuration that has been little explored.

The persistence of ecological variety through mass extinctions

Although species richness and functional diversity have evidently declined in parallel to form today’s latitudinal trends, the two diversity components are strongly discordant across previous mass extinction events. The two era-defining mass extinctions—the

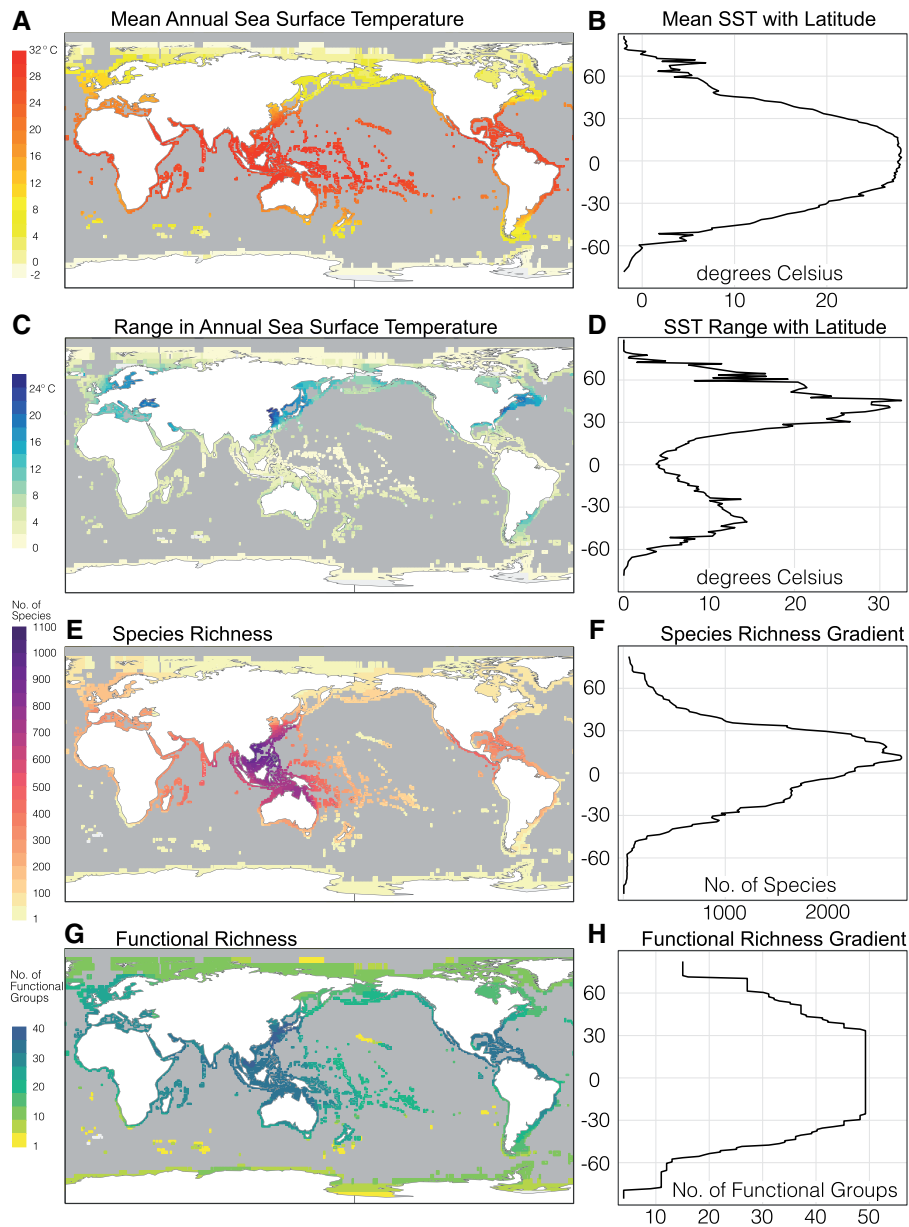


Fig. 3 Present-day patterns in sea-surface temperature with taxonomic and functional diversity patterns of marine bivalves that occur along the continental shelf (water depths 0–200 m). **A**) Mean annual sea surface temperature (SST) within 111-km² equal-area grid cells ($\sim 1^\circ$ of latitude at the equator); data sourced from [Sbrocco and Barber \(2013\)](#). **B**) Mean annual SST average across 1° latitudinal bands shows a broad peak of nearly 30°C across tropical latitudes. **C**) Range in SST binned as in Panel A; data sourced from [Sbrocco and Barber \(2013\)](#). **D**) Annual range in SST is at its lowest near the equator and at polar latitudes, peaking in both northern and southern cool temperature latitudes. **E**) Species richness of marine bivalve genera binned as in Panel A. **F**) Summed occurrences of distinct species across 1° latitudinal bands reveal a broad richness peak within the tropics that declines toward both poles. **G**) Functional richness, the number of distinct functional groups as defined in [Supplementary Table S3](#), per equal area grid cell. **H**) Functional richness nearly saturates globally across the entire tropical and warm temperate zones, declining toward both poles. Distribution data and functional classifications updated from [Edie et al. \(2018\)](#). Color figure available in online version of paper.

end-Permian and the end-Cretaceous—removed an estimated 80–90% and 60–70% of marine bivalve species richness, respectively ([Stanley 2016](#)) and are thus comparable to the size of the climate-driven gradient in bivalve species richness from the tropics to the poles today along different coastlines. However, these mass extinctions removed few, if

any, functional groups ([Erwin et al. 1987](#); [Foster and Twitchett 2014](#); [Edie et al. 2018](#))—an emerging pattern across other extinction events as well (e.g., [Dunhill et al. 2018](#)). Functional group survival through these two mass extinctions cannot be explained by a random loss of taxa ([Edie et al. 2018](#)), which indicates that their persistence may

be tied to a combination of their ecological attributes or the attributes of their constituent taxa. Metabolic-based adaptations also do not appear to have promoted functional group survival as both large body sizes and high-energy feeding types such as suspension feeders survived within the taxonomically-poor functional groups, and no geographic refugia have been detected at the provincial scale that might have shielded the full functional variety from the extinction drivers (Edie et al. 2018). The persistence of trophic resources through the extinction events or a more piecemeal effect of a few wide-ranging, and thus extinction-resistant taxa within each functional group, might have aided in the survival of low diversity functional groups, but the role of such factors remain untested for these events along the functional dimension.

One likely implication of the contrast between the biotic effects of a 70–90% drop of species numbers with latitude (and therefore with climate) today and the estimated 70–90% drop of species numbers in the geologic past is that the mass extinctions were not strongly caused by climate changes of the type or scale that have shaped the latitudinal diversity gradient over the Cenozoic. This leaves us with the question: how will climate change interact with the other accelerating pressures in today's oceans? Projections of rapid temperature changes globally but especially at high latitudes may surpass rates and magnitudes that elevated extinction through the Cenozoic (Pachauri et al. 2014), raising the possibility of similar levels of taxonomic loss in the future.

Outlook

While a large and growing ecological and evolutionary literature addresses the responses of species to anthropogenic climate change (e.g., Urban 2015; Scheffers et al. 2016; Urban et al. 2017), we know relatively little about how such changes impact other aspects of biodiversity such as functional diversity, especially for marine invertebrates. For example, high-latitude species and functional groups of marine bivalves are particularly at risk for climate-mediated extinctions (Valentine et al. 2008; Krug et al. 2010; Jablonski et al. 2017), but how such losses would affect taxonomic and functional diversity of other marine clades deserves more attention. Marine and terrestrial clades appear to have higher functional evenness (i.e., taxa evenly distributed among functional groups) and lower functional redundancy (i.e., fewer taxa per functional groups) at high relative to low latitudes (Schumm et al. 2018), making their persistence more vulnerable to losses in

taxonomic diversity (e.g., Halpern and Floeter 2008). However, the nested structure of both taxonomic and functional richness, with all bivalve functional groups and most supraspecific taxa present in the tropics (Jablonski et al. 2013; Tomašových et al. 2016), may ameliorate global losses by retaining taxa and groups in a tropical reservoir even if they are lost at high latitudes. Indirect effects of climate change could still be severe, when biotic interactions are taken into account (Condamine et al. 2013). Thus, under warming scenarios, latitudinal expansion of tropical functional groups can introduce novel predators, competitors, and parasites that are likely to impact recipient biotas (e.g., Aronson et al. 2015).

Turning to the Cenozoic fossil record, we find that at the global scale, both the magnitude and rate of temperature change have relatively subtle but significant effects on the turnover of marine bivalve lineages. With respect to functional diversity, the clearest evidence shows that the long-term ratcheting effects of climate changes shaped the current latitudinal gradient in functional and taxonomic richness through the loss of taxa and their ecological variety at high latitudes. The effects of shorter-term, pulsed climatic events are less clear, particularly given the evidence that even large diminutions in taxonomic diversity can have very different functional consequences.

Paleontological data offer an opportunity to assess how climate and other environmental factors interact to determine the fate of lineages, but there is no perfect analog for the diverse pressures the marine realm faces today. Robust predictions of biotic response will thus require an array of analyses from a comparative paleontological library of environmental changes at a variety of temporal and spatial scales. Additional integrated studies of functional and taxonomic diversity are needed, with global studies augmented by detailed analyses of regions subject to contrasting climatic and environmental pressures. Even absent precise analogs to modern conditions, paleobiological analyses can offer insights into multi-dimensional biotic response to the tempo and mode of abiotic changes.

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Supplementary data

Supplementary data available at *ICB* online.

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