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Review

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Review

Perfect storms shape biodiversity in time and space

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ABSTRACT

Many of the most dramatic patterns in biological diversity are created by "Perfect Storms" —rare combinations of mutually reinforcing factors that push origination, extinction, or diversity accommodation to extremes. These patterns include the strongest diversification events (e.g. the Cambrian Explosion of animal body plans), the proliferation of hyperdiverse clades (e.g. insects, angiosperms), the richest biodiversity hotspots (e.g. the New World Tropical Montane regions and the ocean's greatest diversity pump, the tropical West Pacific), and the most severe extinction events (e.g. the Big Five mass extinctions of the Phanerozoic). Human impacts on the modern biota are also a Perfect Storm, and both mitigation and restoration strategies should be framed accordingly, drawing on biodiversity's responses to multi-driver processes in the geologic past. This approach necessarily weighs contributing factors, identifying their often non-linear and time-dependent interactions, instead of searching for unitary causes.

Keywords: biogeography; diversification; extinction; fossil record; hotspots; origination; coldspots; palaeobiology

INTRODUCTION

The Tree of Life is remarkably inelegant: some parts have undergone stochastic pruning and growth, but large branches have been hacked off while others have proliferated far out of proportion to the rest of the tree. The geography of life is also highly uneven, with diversity hotspots and coldspots scattered across the globe, even within single latitudinal or climatic belts. These temporal and spatial patterns have fuelled extensive efforts to identify drivers, with mixed and apparently contradictory results. Such contradictions arise in part because the most dramatic patterns in biological diversity are the products of 'perfect storms' (Junger 1997)—rare combinations of mutually reinforcing factors that push origination, extinction, or diversity accommodation to extremes. Analysing when and where such patterns emerge is critical not only for understanding how biodiversity is deployed in time and space, but also for predicting the impacts of reconfiguring biodiversity through the ongoing Perfect Storm of human activity.

DIVERSIFICATION EVENTS

Multiple diversity-promoting factors have been implicated in the most dramatic proliferations of species or higher taxa, modes of life, or phenotypic disparity. These different dimensions or currencies of biodiversity need not rise in tandem, and this discordance is important to understanding macroevolutionary processes (Foote 1997, Jablonski 2017a, b). The Cambrian Explosion of metazoan life, *c.* 540 Myr ago, stands out as a spectacular pulse in morphological disparity that outpaced the relative origination rate of lower taxa (Erwin and Valentine 2013, Erwin 2021). This singular event has many potential drivers, still much-debated, and isolating a single factor may not be feasible or appropriate. Both the Ediacaran prelude and the Explosion interval occurred across dispersed continents in the context of geological events hypothesized to drive the rise of oxygen in the oceans and favourable ocean chemistry for biomineralization, and an ecological landscape rich in opportunities and positive feedbacks among organisms hypothesized to possess complex but flexible gene-regulatory controls (see Table 1 for references supporting this and other examples below). We suggest that none of these factors alone could have driven the Cambrian event. These physical factors did not revert to pre-Cambrian levels later in the Phanerozoic (except, arguably, continental dispersion—see below), suggesting that the Cambrian evolutionary burst and, equally important, its cessation involved biotic feedbacks as well (as long recognized, e.g. Valentine 1980, 2004).

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In principle, every macroevolutionary Perfect Storm should have corresponding cases that are less dramatic, and thus are potential natural experiments for evaluating contributing factors. The aftermath of mass extinctions should be especially telling because re-diversification failed to generate the phylum-level morphological and ecological novelty seen in the Cambrian (Valentine 2004, Erwin and Valentine 2013). The rebound from the Late Permian event, when species extinction ranged from 80–95% depending on assumptions, would seem to present another Cambrian-level opportunity for diversification into a wide-open ecological landscape, but presumably without such hypothetically flexible developmental systems. However, few adaptive zones were fully vacated here and during the other Big Five extinctions (Erwin *et al.* 1987, Foster and Twitchett 2014, Dunhill *et al.* 2018, Edie *et al.* 2018)—a fascinating pattern that tells us much about the nature of mass extinctions but frustrates attempts to tease apart rival hypotheses for the unique Cambrian Explosion. Analyses of diversification in clades whose adaptive zones came especially close to being fully vacated will still be informative: the failure of stalked crinoids to achieve Palaeozoic levels of morphological disparity in the Mesozoic and Cenozoic may be evidence for the hardening of developmental systems (Foote 1999), although damping effects of novel competitors and predators are difficult to rule out. Teasing apart alternatives may be the wrong way to ask the question.

Another global, richly polyphyletic diversity increase is the Late Mesozoic–Cenozoic rise in marine and terrestrial taxonomic richness (reviewed by Benson *et al.* 2021, Bush and Payne 2021, Benton *et al.* 2022). This increase has been attributed to biotic factors, such as an increase in the frequency, variety, and intensity of predation and other diversity-promoting interactions, increased nutrient input (sometimes viewed in terms of power, i.e. energy per unit time; Vermeij 2019), and abiotic events, including the fragmentation of the Pangaea supercontinent, and later cooling at the poles that steepened temperature gradients, both processes allowing discrete provinces to form along north–south coastlines (see Table 1). One unanswered question is how plate tectonics interacts with climate: do dispersed continents within maximally broad tropics, such as the ice-free world of the Mid-Miocene Climatic Optimum, accommodate or promote more diversity compared to times when the poles are (modestly) refrigerated to produce a narrower tropical zone but a greater number of discrete biogeographic provinces, as in Pleistocene interglacials? Dips in Latest Cenozoic diversity seen in some analyses (see references above) may be analytical 'edge effects', but may also be a genuine biotic signal.

HYPERDIVERSE CLADES

The prolific taxonomic diversification of individual clades has often been attributed to 'key innovations'—novel traits that open up new ecological opportunities (or that simply promote rapid speciation without ecological expansion, a very different mechanism). However, the rise of the richest clades is likely tied to a combination of multiple intrinsic and extrinsic factors, which may or may not need to appear in a particular sequence (Losos 2010, Bouchenak-Khelladi *et al.* 2015, Donoghue and Sanderson 2015). For example, the lists of factors thought to have facilitated the extraordinary diversifications of angiosperms and insects are remarkably long (Table 1). Notable in both of these groups is not just their propensity to generate and accumulate species, but their phenotypic evolvability, exploring novel functions and morphologies (Jablonski 2022). Diversification of either group has yet to be fully analysed in the latter two dimensions, but there are tantalizing hints of their discordance and thus their putative causes, e.g. evidence that nearly the full array of insect mouthparts had been achieved prior to angiosperm diversification (Labandeira 2019). Thus, while both host diversification and feeding specializations doubtless promoted the proliferation of insect species (see Albrecht *et al.* 2023), many basic feeding adaptations were evidently in place too early to fit classical co-evolution scenarios. Perhaps insect herbivory, along with associated pollination syndromes, contributed to the initial diversification of angiosperms (Crepet and Niklas 2009). Understanding these two hyperdiverse clades, likely coupled as they are, would account for an impressive fraction of multicellular life on Earth.

As with the Cambrian Explosion, comparisons to less extreme examples may be fruitful. If truly prolific diversification requires the confluence of multiple factors, this may explain, statistically speaking, why most clades are of moderate to low diversity throughout their histories, and comparative analyses of those clades can pinpoint factors absent in their histories but present in richer sister groups. The great diversity and disparity of the prolific clades may actually derive from independent diversification of certain subclades within them, further highlighting the scarcity and context-dependence of evolutionary Perfect Storms. The exceptional diversity of orchids and hymenopterans within angiosperms and insects, for example, bears continued investigation, and many such instances also appear attributable to the simultaneous operation of multiple reinforcing factors (Table 1). However, analysis of key traits or sequential trait acquisition is complicated by extinction, which can condense multiple events to a few nodes within a pruned evolutionary tree. The pervasiveness of extinction in deep time also requires careful evaluation of among-clade diversity contrasts: some clades have always resided at low diversities or disparities (Bennett *et al.* 2017, Caron and Pie 2022, note this fits the 'survivor clade' model of Gould and Eldredge 1977), but the dead-clade walking phenomenon is also widespread, where once-diverse clades were bottlenecked in extinction events or via slower attrition (Jablonski 2002, 2022, Barnes *et al.* 2021). The fossil record is a critical testing ground for distinguishing these scenarios.

The probabilistic nature of Perfect Storms may also explain the macroevolutionary lags between the first fossil occurrence of many clades and their diversifications (Jablonski 2017a, Kröger and Penny 2020). Even major clades that originated in the Cambrian lay fallow for tens of millions of years, such as Bivalvia and perhaps Chordata: their quiescence and subsequent diversification has been attributed to a lag in the acquisition of one or more additional traits that enabled what eventually became taxonomically, functionally, and morphologically spectacular radiations (Brazeau and Friedman 2015, Zhou *et al.* 2023). Thus, the traits present at the inception of these groups were evidently insufficient to enable their eventual diversification. Comparative analyses that dissect the sequence of evolutionary events may shed light on proximate triggers vs. the foundations of major diversifications.

Table 1. Factors potentially underlying Perfect Storms of biodiversity.

Patterns	Potential interacting factors	References
Diversification events		
Cambrian	Oxygen; nutrients; continental fragmentation; initial ecological opportunity; biotic interactions; developmental capacity	Brennan *et al.* 2004, Marshall 2006, Erwin and Tweedt 2012, Erwin and Valentine 2013, Na and Kiessling 2015, Sperling and Stockey 2018, Wang *et al.* 2018, He *et al.* 2019, Erwin 2021
Late Mesozoic–Cenozoic	Nutrients; continental fragmentation; biotic interactions; climate	Valentine and Moores 1970, Valentine *et al.* 1978, Allmon and Martin 2014, Zaffos *et al.* 2017, Vermeij 2019, Benson *et al.* 2021, Benton *et al.* 2022, Bush and Payne 2021, Cermeño *et al.* 2022
Biogeographic hotspots		
West Pacific	Warm temperatures; low seasonality; large, two-dimensional but discontinuous habitat area; topographic complexity; intense biotic interactions; specializations	Rosen 1984, Hoeksema 2007, Mittelbach *et al.* 2007, Leprieur *et al.* 2016, D Huang *et al.* 2018
Tropical Montane	Low seasonality; topographic and other environmental complexity; large but discontinuous habitat area; intense biotic interactions; specializations	Mittelbach *et al.* 2007, Fine 2015, Badgley *et al.* 2017, Antonelli *et al.* 2018, Pellissier *et al.* 2018, Rahbeck *et al.* 2019, Tenorio *et al.* 2023
Cape Flora	Damped glacial–interglacial fluctuations; heterogeneity of topographic and moisture conditions	Jansson and Dynesius 2002, Van Santen and Linder 2020, van Mazijk *et al.* 2021
Temperate West Pacific	Proximity to tropical West Pacific (see above); nutrients	Jablonski *et al.* 2017, Vermeij *et al.* 2019
Biogeographic coldspots		
Antarctica	Cold temperatures; seasonality; isolation; extinction	Krug *et al.* 2010, Crame 2018, 2020, 2023
Tropical East Atlantic	Isolation; smaller, less complex, and linear habitat area; extinction	Vermeij 1978, 2012
Central Atacama Desert	Low moisture; low nutrients; low environmental heterogeneity; high temperature variation; high UV radiation	Eshel *et al.* 2021 (but not for microbes, see Gómez-Silva and Batista-García 2022)
Hyperdiverse clades		
Angiosperms, and certain subclades	Whole-genome duplications and hybrid polyploidy; homeotic gene effects; asexual/sexual reproduction; annual life cycles; biotic interactions with fungal and animal lineages; entry into new environments; major climatic or tectonic events	Crepet and Nicklas 2009, Givnish *et al.* 2015, Sauquet and Magallón 2018, Vamosi *et al.* 2018, Benton *et al.* 2022
Insects, and certain subclades	Biotic interactions with plant and animal lineages; specialization; sociality; modular development	Mayhew 2007, 2018, Condamine *et al.* 2016, McKenna *et al.* 2019, Labandeira 2019, Blaimer *et al.* 2023
Teleosts, and certain subclades	Whole genome duplication (with macroevolutionary lag); mass extinction of competitor; pharyngeal jaws and cranial kinesis	Alfaro *et al.* 2009, 2018, Larouche *et al.* 2020, Davesne *et al.* 2021, Ghezelayagh *et al.* 2022, Friedman 2022
Rodents	Small-bodied/short generation times; weak species-level dispersal but repeated clade-level invasions of new regions; high population growth rates; mainly herbivorous diet; continuous incisor growth; 'opportunistic feeding strategies'	Stanley 1990, Wilson and Sanchez-Villagra 2010, Alhajeri and Steppan 2018a, b
Extinction events		
End-Cretaceous	Impact; volcanism; impacted rocks; low sea level	Sigurdsson *et al.* 1992, Peters 2005, Schulte *et al.* 2010, Chiarenza *et al.* 2020, Hull *et al.* 2020, Junium *et al.* 2022
End-Permian	Volcanism; intruded rocks; continental assembly; low sea level	Peters 2005, Bond and Grasby 2017, Clapham and Renne 2019, Elkins-Tanton *et al.* 2020, Chapman *et al.* 2022, Saito *et al.* 2023
Anthropocene (impending)	Exploitation; habitat loss and fragmentation; pollution; biotic interchange; ocean acidification	Dirzo *et al.* 2014, Kidwell 2015, Price 2022, Pörtner *et al.* 2023

BIOGEOGRAPHIC HOTSPOTS

The composite global curves often used to depict latitudinal diversity trends belie the uneven spatial distribution of diversity hotspots and coldspots. These concentrations and apparent deficits of biodiversity are another source of insight into factors driving the origin and accumulation of different macroevolutionary currencies. Here too, the most extreme cases appear to derive from mutually reinforcing factors (Gaston 2000, Jablonski *et al.* 2017).

Several terrestrial hotspots occur within the tropics, but in the ocean one towers above the rest: the tropical West Pacific, and within that the Coral Triangle, combining a strong spatial dynamic involving the influx of taxa from other tropical regions with an array of *in situ* factors, including intense biotic interactions, warm temperatures, low seasonality, and the intersection of four major geologic plates driving a complex island-mainland structure across a vast area containing many habitat types (reefs and mangroves to lagoons and open shelves). The age of the tropics in general, and therefore their inferred long-term stability relative to extratropical settings, has also been invoked as a contributing factor, but it is not clear whether this 'time hypothesis' can enter into mechanisms driving the formation of marine diversity hotspots (see Table 1).

Terrestrial diversity hotspots are underlain by similar suites of mutually reinforcing factors. Here, the environmental complexity derives from tectonics, particularly mountain-building, with a steeper latitudinal gradient going along mountainous regions than across lowlands. In terrestrial settings, tropical species tend to have narrow thermal tolerances, with accompanying narrow geographic ranges, contributing to hotspot richness (Polato *et al.* 2018); the pattern is more complex in marine systems, where narrow thermal tolerances can be accompanied by broad distributions as species track widespread temperatures (Tomašových *et al.* 2015). Direct palaeontological data are localized, but suggest that mountain-building during climate optima may be most productive in terms of diversification (Badgley *et al.* 2017, Weaver *et al.* in press), raising the possibility that, as suggested for marine diversity, terrestrial global and hotspot diversity has declined from a Mid-Miocene or Pliocene maximum. As with temporal patterns, however, different macroevolutionary currencies may not be spatially congruent (Oliveira *et al.* 2016, Schumm *et al.* 2019). More than twice as many biomes are needed to capture half of the global phylogenetic diversity of vascular plants compared to half of their species richness (Tietje *et al.* 2023).

The evolutionary dynamics of diversity hotspots, and of latitudinal gradients in general, have also proven to involve interactions among factors. The long-standing question of whether the tropics are a cradle or museum of biodiversity is evidently a false dichotomy. Although in principle diversity peaks could be generated solely by either low extinction rates or high origination rates, the tropics appear to be both a generator and an accumulator of diversity (Jablonski *et al.* 2006, 2017, Crame 2020, Vasconcelos *et al.* 2022), and, outside the tropics, a similar argument has been made for the Cape Flora (Verboom *et al.* 2009). Testing these models is difficult. In palaeontological data, the post-Palaeozoic fossil record is generally under sampled in tropical settings, which can distort apparent latitudinal gradients and dynamics over time (Allison and Briggs 1993, Jablonski *et al.* 2006, Valentine *et al.* 2013, Crame 2020, Jones *et al.* 2021, the under sampled tropics is also a problem for quantifying present-day diversity, see Freeman and Pennell 2021, Rudbeck *et al.* 2022). The tropical origin followed by latitudinal range expansion out of the tropics recorded for marine bivalve genera is thus in opposition to this bias and probably underestimates the prevalence of the out-of-the-tropics dynamic, at least in this clade. For neontological data, inference and time-calibration of ancestral biogeography requires strong assumptions, not least being that the present-day distributions of taxa accurately reflect the point of origin and subsequent extent. This may be a reasonable assumption for very young species, although the past 2 Myr have seen dramatic, repeated glacial–interglacial range shifts (Williams and Jackson 2007, Willis and MacDonald 2011). For older clades, carefully considered palaeontological data can reveal very different biogeographic dynamics than can be inferred from present-day distributions (for numerous examples, see Herrera *et al.* 2015, Wisniewski *et al.* 2022). Clearly the way forward is improved integration of palaeobiology and present-day phylogenies.

BIOGEOGRAPHIC COLDSPOTS

Diversity coldspots raise another set of questions, foremost whether their low richness across many biodiversity dimensions results from either the active suppression or lack of promoting factors. If coldspots are defined relative to the median expected diversity for their latitude, elevation, bathymetry, or other environmental variable of interest, we can then ask whether extreme values of a single key factor push regions to anomalously low diversity levels, or if they, too, operate as Perfect Storms. For example, the non-random distribution of deserts across the globe suggests an intersection of mutually reinforcing physical factors: concentration along the tropical–extratropical border, where water-stripped atmospheric downdrafts from Hadley cell convection continue their desiccation across mountain rainshadows and/or cold upwelling zones along coastlines. The hyperarid core of the Atacama Desert enjoys relatively mild mean annual temperatures but is so dry and nearly abiotic that it can serve as a model for the Mars environment (Navarro-González *et al.* 2003).

Evolutionary dynamics are likely to differ between hotspots and coldspots, given that coldspots not only harbour fewer species, but fewer species per genus than either hotspots or 'average' regions (e.g. Le Roux *et al.* 2019). Coldspots may also contain a greater proportion of endemic taxa (Le Roux *et al.* 2019, Qian *et al.* 2023), suggesting greater per-taxon extinction risk, although this difference will depend on the relative contribution of geographic-range overlap and endemism to hotspot richness. As with hotspots, different currencies of biodiversity may be discordant going from 'average' regions into coldspots, for example taxonomic diversity vs. phylogenetic diversity (e.g. Qian *et al.* 2023), or diversity vs. within-region turnover or beta-diversity (Price 2002). Today's refrigerated poles are geologically young environments (reviewed by Crame 2023); perhaps given time, today's coldspots will gain richness even if conditions remain constant (a highly unlikely scenario). However, for some coldspots, certain physical drivers regularly fall outside the physiological capabilities of most clades (as noted by Willig *et al.* 2003), suggesting that low regional diversities are not simply a function of age. Again, these biologically anomalous regions are best analysed via improved integration of phylogenies with direct observations of regional diversity changes in the fossil record.

EXTINCTION EVENTS

Much of the literature on major extinction events has entailed the search for a single driver, if not for all of the events then at least for a single factor behind each of the 'Big Five' mass extinctions (e.g. D Sepkoski 2020). However, virtually all of the hypothesized drivers have occurred at other points in time without such powerful biotic consequences—even extraterrestrial impacts and massive volcanic eruptions. Of course, impacts and massive volcanism each produce a plethora of (similar) extinction drivers, including darkness, cold followed by greenhouse warming, acid rain, and ocean acidification, wildfires, ozone destruction, and so on (references in Table 1). However, the end-Permian eruptions occurred in the context of other factors destabilizing climates, including exceptionally low sea levels, and the end-Cretaceous impact occurred in close association with Deccan volcanism, again at a time of relatively low sea levels. The local geological context of these events may also have exacerbated their effects: the end-Palaeozoic Siberian Traps intruded into coal-rich sediments, increasing sulphur and carbon emissions, and the end-Cretaceous Chicxulub bolide struck marine evaporites, also increasing the sulphur content of the resulting plume (Sigurdsson *et al.* 1992, Retallack and Jahren 2008, Elkins-Tanton *et al.* 2020). Major extinctions may in part derive from the alignment of similar proximate causes, albeit with different triggers, but the compounding effects of other, more contingent factors may have tipped the balance.

The many smaller but apparently global extinction pulses throughout the fossil record (Bambach 2006, but see Foote 2007 on backwards-smearing as an artificial source of some small events) could be the basis for comparative analyses, allowing potential drivers to be weighed or factored out (see also Lockwood 2008). For example, the abrupt warming of the Palaeocene–Eocene Thermal Maximum (PETM) drove far more spatial shifts than global extinctions (Foster *et al.* 2020, Hupp *et al.* 2022), but the inferred hyperthermal aspects of the end-Permian and end-Cretaceous events are held to be critical components of those extinctions. These contrasts suggest either that we do not understand the timing or severity of inferred warming during the mass-extinction events, or, more likely, that warming alone cannot push most clades to the breaking point.

THE ANTHROPOCENE IS A PERFECT STORM

The human impact on the Earth and its inhabitants is a Perfect Storm, said by many to constitute a new geologic interval termed the Anthropocene. Marine and terrestrial systems are being subjected to climate change, habitat destruction, pollution, species introductions, and over-exploitation, quite possibly all at once, with many additional specific factors affecting each system, such as ocean acidification and anoxia. Although the spatial scale of these stressors ranges from global to highly localized, the net effect is truly worldwide (even Antarctica and Tibet receive toxic levels of per- and polyfluoroalkyl substances (PFAS), Cousins *et al.* 2022). Analyses of the very young fossil record show that myriad anthropogenic effects were underway prior to the establishment of direct scientific observations or baselines in many regions (Jackson *et al.* 2001, Kidwell 2015, Nawrot *et al.* 2023).

Leaving aside direct societal effects, these anthropogenic pressures are driving extensive evolutionary and biogeographic responses in the world's biota, along with a poorly known degree of population- and species-level extinction. The aggregate effect has yet to approach the Big Five mass extinctions of the geologic past, but the multidimensional, mutually reinforcing nature of the Anthropocene pressures is reminiscent of past Perfect Storms, and many of the drivers of past extinctions are shared with those in action today (Kiessling *et al.* 2023). One undeniable message from past events is simply that clades and ecosystems do have tipping points, with downstream consequences that have been extreme, global, and long-lasting, with winners and losers that need not match human interests. The precise nature of these tipping points, and their macroevolutionary consequences, are an area of active study (e.g. Jablonski 2017b, Pyron and Pennell 2022).

The Perfect Storms perspective may allow more nuanced and specific applications of our characterization of past events to the present day, even if today's combination of pressures is in some ways unprecedented. For example, the muted extinction seen for most of the clades and ecosystems in response to the PETM suggests that warming alone would not create a biotic crisis today *if* species could shift their geographic ranges accordingly, as they evidently did during the PETM and other warming intervals, including glacial–interglacial cycles (Willis and MacDonald 2011). Past patterns thus strongly support the expansion of marine and terrestrial reserve networks that encompass spatial and elevational climate gradients and are designed to strengthen connectivity among those reserves (Gupta *et al.* 2019, Arroyo-Rodríguez *et al.* 2020, Pörtner *et al.* 2023). (Of course, such measures would not address the societal costs of spatial shifts in the ranges and phenologies of pests, shifting precipitation patterns, sea level rise, and other consequences of warming that the natural world has accommodated many times over.) Differential responses of clades to past Perfect Storms can also inform conservation efforts, for example by combining key indicators, such as current geographic range sizes, current temperature tolerances, and past clade-level volatility, as a gauge for modern extinction risk, an especially urgent need for groups lacking extensive IUCN assessments (Collins *et al.* 2018, S Huang *et al.* 2023). The most intriguing questions, which become urgent with real-world consequences, may lie where different Perfect Storms give contrasting expectations. For example, functional diversity parallels the drop in taxonomic diversity from today's tropical biodiversity hotspots into high latitudes, but barely decreases at all across mass extinctions that deplete taxonomic diversity to an extent comparable to the modern latitudinal gradient (Edie *et al.* 2018).

APPROACHES TO PERFECT STORMS

The search for unitary mechanisms is a valuable means of sharpening hypotheses and discarding the weaker ones, but the most dramatic patterns in biodiversity are generated by diverse, mutually reinforcing drivers. Such multifactorial explanations do not mean that we cannot rank drivers in particular cases, but they indicate that comparative analysis and synthesis can yield new insights—why the other mass extinctions were less severe than the end-Permian one, why the recovery from the end-Permian extinction was less dramatic than the Cambrian Explosion, why the Cape Flora is richer than the Patagonian one, why squamates and birds are less diverse today than bony fishes and insects—and new approaches to integrating fossil and present-day data are likely to be key to our understanding.

In principle, it is possible to model, or at least conceptualize, multicausal diversity patterns. Thus, for marine biodiversity, in strictly abiotic and ahistorical form, we might model tropical provinces in these terms: warm temperatures + low seasonality + broad area + discontinuous habitats = West Pacific diversity levels; whereas warm temperatures + low seasonality + narrow area with more continuous habitats = East Pacific diversity levels. These formulations are insufficient, however, as a Plio-Pleistocene extinction term is probably required to account for lower diversity in the Caribbean than in the tropical East Pacific, and a proximity-to-the-West-Pacific term is probably required to account for lower diversity in the Caribbean than in southern Japan and south-east Australia (Jablonski *et al.* 2017). Both of those additional terms imply a significant role for non-equilibrium dynamics at the regional level. Further, these geographic inequalities hold not just for present-day taxonomic richness, but for historical patterns in the origins of evolutionary novelties (Vermeij 2023). The generally loose correlations among taxonomic richness, phenotypic disparity, and functional variety (Jablonski 2017b) almost certainly demand additional terms in a multi-level, and spatially nested, expansion of this basic framework. New computational and methodological advances combine generative and predictive models that weigh potential drivers of biodiversity (Rangel *et al.* 2018). Such models will require comparative biogeographic and phylogenetic analyses to evaluate the hierarchical level, spatial scale, and the sequence in which potential factors have operated or interacted to make observed patterns, including the times and places where factors interfere and cancel each other out (e.g. negative effects of habitat area damping positive effects of temperature dynamics to yield East Pacific diversity, as above).

The first-order differences among extinction events may operate in similar ways: predictable in broad terms, so that more compounding negative pressures equal more biodiversity loss, but the particulars of survivorship, loss, and rebound are much more complex. Global biotas and their traits change through time, along with the nature and intensities of extinction drivers (Foster *et al.* 2023). One question that has received virtually no attention is how different combinations of drivers could shape extinction rebounds: the biotic response should reflect the different time constants or spatial scales of the compounding drivers. Apparent lags and asynchrony among post-extinction rebounds probably reflect some combination of sampling, persistence of one or more adverse factors that unevenly affect surviving clades, and clade-specific dynamics, as in the near-instantaneous rebound of the Early Triassic ammonoids relative to other groups (e.g. Pietsch *et al.* 2019). Thus, clade proliferation also may be predictable in broad terms, in that certain traits tend to promote higher speciation rates (see Jablonski 2008), but the interactions among traits and environmental context that allow clades to break the 'macroevolutionary trade-off', in which factors that enhance speciation rates also elevate extinction rates (Stanley 1979, 1990, J Sepkoski 1998, Jablonski 2006, 2017b), or to reduce diversity-dependent feedbacks (Foote 2023), remain poorly understood. Contingencies in time, space, and biology may prevent macroevolutionary Perfect Storms from being predictable in the way meteorological ones can be, at least in terms of the confluence and relative effect sizes of the particular drivers, but a shift toward emphasizing the complexity of these rare evolutionary events will almost certainly improve our understanding of their origins and biological consequences.

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