Climate as a Driver of Evolutionary Change   Review

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The link between biodiversity and climate has been obvious to biologists since the work of von Humboldt in the early 1800s, but establishing the relationship of climate to ecological and evolutionary patterns is more difficult. On evolutionary timescales, climate can affect supply of energy by biotic and abiotic effects. Some of the best evidence for a link between biodiversity and climate comes from latitudinal gradients in diversity, which provide an avenue to explore the more general relationship between climate and evolution. Among the wide range of biotic hypotheses, those with the greatest empirical support indicate that warmer climates have provided the energetic foundation for increased biodiversity by fostering greater population size and thus increased extinction resistance; have increased metabolic scope; have allowed more species to exploit specialized niches as a result of greater available energy; and generated faster speciation and/or lower extinction rates. In combination with geologic evidence for carbon dioxide levels and changing areas of tropical seas, these observations provide the basis for a simple, first-order model of the relationship between climate through the Phanerozoic and evolutionary patterns and diversity. Such a model suggests that we should expect greatest marine diversity during globally warm intervals with dispersed continents, broad shelves and moderately extensive continental seas. Demonstrating a significant evolutionary response to either climate or climatic change is challenging, however, because of continuing uncertainties over patterns of Phanerozoic marine diversity and the variety of factors beyond climate that influence evolution.

Introduction

Beginning with Alexander von Humboldt, 19th Century naturalists recognized latitudinal gradients in species richness on land and sea [1,2] and speculated about the relationship between climate and evolution. Climate can have a variety of different effects on speciation and extinction rates, diversity levels and other evolutionary patterns and processes. Latitudinal gradients are the most obvious connection between climate and evolution, and provide the best explored system relating climate to evolutionary change. Thus, we can employ our understanding of latitudinal diversity gradients to examine this relationship. These gradients have now been documented in some 600 studies across a variety of scales, habitats and taxonomic groups [3,4] and have been recognized through the Mesozoic (252–65 million years ago (Ma)) and into the Paleozoic [5–7] (542– 252 Ma), although the slope of the gradients may have changed over time and there is no certainty that latitudinal diversity gradients persisted throughout the last 542 million years. While some relationship between species richness

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and the amount of energy available seems clear, the relationship between energy, climate, latitude and diversity is complex [4,8–11].

Recent global warming has demonstrated that organisms respond to climate and climatic change in a variety of ways, depending on the nature, rate and duration of the change, and the range of available biological responses [12]. Niche conservatism for climatic factors appears to be widespread, based on evidence showing that many closely related species occur in similar climates and are resistant to moving into novel climatic environments. Since species within a community often differ in their degree of niche conservatism [13,14], climatic changes will ripple through communities, disrupting ecological relationships as species migrate or disappear to differing degrees. Although these changes will influence biogeographic shifts as seen in the fossil record, it may often be difficult to determine whether such a range shift was a shift of the realized niche with persistent niche conservatism, or an adaptive evolutionary response.

Over the past four billion years, the Earth has experienced far greater climatic variability than observation of the past few million years would ever suggest. Viewing the relationship between climate and evolution through a broader temporal perspective emphasizes uncertainties over whether climate exerts its influence on evolution through climatic change, climatic variability, or long periods of climatic stasis. Moreover, in some cases several climatic events may well have been biologically mediated, with climate change as the consequence of evolution rather than its cause. For example, the massive, worldwide glaciation some 2.3 billion years ago may have been induced by the origin and spread of cyanobacteria, and oxygenic photosynthesis [15]. Although the causes of this Great Oxidation Event remain controversial, under this hypothesis, cyanobacteria destroyed a methane greenhouse that dominated the Archean Era (4.0–2.5 billion years ago) and triggered an irreversible shift in the oxidation state of the Earth's oceans and atmosphere. Similarly, during the Neoproterozoic (1000–542 Ma) the Earth experienced multiple extensive, perhaps global, glaciations, with the final glaciation immediately preceding the rise of animals, and during the glaciations the diversification of various eukaryotic groups and early animals may have altered the carbon cycle sufficiently to affect climate.

Other climatic events of the Phanerozoic, if not biologically mediated, certainly represent climatic variability outside our understanding of the past few million years. These include the brief end-Ordovician glaciation during a severe mass extinction, the long Permo-Carboniferous glaciations, prolonged warming during the Mesozoic and repeated climatic perturbations through the past 65 million years, all of which have been invoked as drivers of evolutionary change [16]. A rich history of studies relate Pleistocene glaciations to shifting plant and animal distribution, invoke climate change as a driver for human evolution and posit climatic amelioration as facilitating the rise of agriculture.

In this review, I am primarily concerned with whether climate has had a demonstrable, longer-term effect on taxonomic diversity and evolutionary innovation, principally in the marine realm. While the number of taxa is but one component of diversity [17], a more robust record exists of
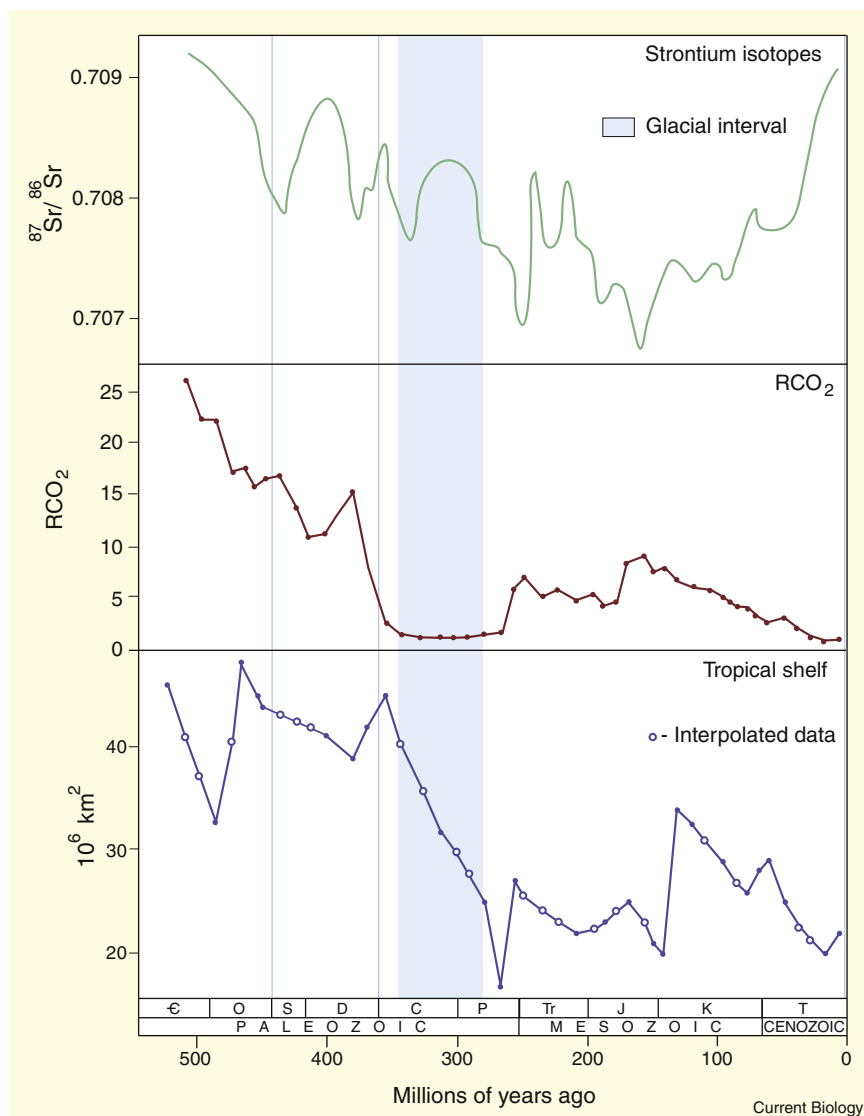
Figure 1. Phanerozoic patterns of climatically relevant indicators.

Middle panel: atmospheric CO_2, a significant green house gas [75]; top panel: strontium isotopic ratios, reflecting the relative degree of continental weathering, which reduces atmospheric carbon dioxide versus the activity of tectonic spreading centers along the mid-ocean ridges [106]; bottom panel: tropical shelf area [60] reflecting the amount of area available for occupation in high energy environments. Data were recalibrated for the bins shown in Figure 2. (C: Cambrian; O: Ordovician; S: Silurian; D: Devonian; C: Carboniferous; P: Permian; Tr: Triassic; J: Jurassic; K: Cretaceous; T: Tertiary.)

taxic diversity patterns than of the other components of evolutionary history. I begin with a discussion of the abiotic influences of climate before turning to energy, the currency through which climate impacts biology. Most studies of the biotic effects of climate have involved latitudinal diversity gradients, so a discussion of these general principles can be evaluated against the empirical record. After a discussion of the pitfalls of a general comparison of climate and Phanerozoic (542 Ma–present) diversity, I turn to specific intervals where more robust studies have been produced. I close by returning to the relationship between climate change and evolution, with suggestions for future directions.

Abiotic Responses to Climate

The distribution of the continents exerts a first-order control on global climate through their influence on chemical weathering, atmospheric and oceanic circulation patterns and the albedo, or reflectivity, of the planet. As plate tectonics alter the positions of the continents, their topography and their relationships, it affects the amount of continental area in the tropics and the height of mountain ranges. Sea-floor spreading rates influence sea-level by generating hotter, less dense oceanic crust, shallower ocean basins and usually more epicontinental seas. The amount of shelf-area in low latitudes has varied considerably through the Phanerozoic (Figure 1). If the area of the shallow tropics was a first-order control on the diversity of marine benthic organisms, this variation in shelf area should have had a major impact on diversity. Moreover, the weathering rates of mountains (specifically, silicate rocks such as granites) are greater in the tropics, thus drawing CO_2 out of the atmosphere. Global warming will increase continental weathering rates, reduce the oxygen saturation of the oceans and may eventually shift oceanic circulation and upwelling patterns. But by drawing down CO_2, a negative feedback loop is created that eventually limits the warming. Continents also have greater albedo than the open ocean, such that more continental mass at low latitudes will decrease the overall energy budget of the Earth relative to continents at higher latitudes, possibly moderating biotic diversity. Strontium isotope ratios are an index of the relative influx of strontium from weathering of granitic rocks versus from sea-floor spreading, and provide an imperfect index of weather rates and their relationship to climate (Figure 1).

Regional conditions can also have a strong impact on climate and biodiversity. For example, Middle Miocene marine diversity along the California coast largely reflected the development of a strong upwelling system, bringing up cold, nutrient-rich waters from the deep sea, and led to the diversification of a variety of kelp, birds, fish and invertebrates [18]. The strength and persistence of the upwelling reflected the particular tectonic and climatic setting of western North America during the Miocene, but similar strong upwelling regimes have occurred in the past in other regions. Continental positions will also influence oceanic and atmospheric circulation patterns. For example, today's north-south alignment of the continents and the absence of a circum-equatorial current funnel more heat into higher latitudes than would otherwise be the case.

Thus, the indirect, abiotic effects of climate change on organisms may have been substantial. Although these factors have been operating throughout the Phanerozoic, their effects are best understood in the Cenozoic (65 Ma–present). For example, several different groups of plankton exhibited increases in body size during climatic cooling, including deep sea ostracodes [19] and planktic foraminifera [20], while there was a decrease in body size of dinoflagellates, diatoms and coccolithophorids [21], apparently due to altered circulation patterns produced by an increase in the latitudinal thermal gradient (although see [22] for a different view). Today, increasing temperatures are impeding the growth of the coral *Porites* on the Great Barrier Reef in Australia by increasing pH and reducing carbonate saturation rates [23]. Here climate change has reduced calcification rates, likely leading to a decline in the integrity of the reef [24].

Energy, Latitude and Diversity

Averaged over the year, the energy received in the tropics is only four times as great as at the poles [25], although the seasonality and intensity of the incident radiation obviously vary greatly. Still, this energy differential is far less than the difference in diversity. Clarke and Gaston [26] distinguish three different types of energy: photosynthetically active radiation, the part of the visible spectrum utilized for photosynthesis, which peaks at low latitudes; Gibbs free energy, the chemical energy released by the oxidation of organic compounds during metabolism; and thermal energy, generally measured by temperature, which also peaks in low latitudes. Although each energy type differs in its impact on biodiversity, many discussions of species–energy relationships fail to discriminate between them. Temperature is often used as a metric of energy, but temperature is not energy and cannot be used by organisms, as is obvious from the fact that two bodies at the same temperature may have very different thermal capacities. Thermal energy, rather than temperature, often limits organismal distribution, particularly of marine larval stages, because of physiological limits to growth and survival, and the boundaries of marine provinces often reflect points where temperature changes rapidly [27]. For terrestrial vascular plants, there is little relationship between photosynthetically active radiation and diversity, but a strong relationship between water availability and temperature, which together influence diversity [16]. For heterotrophic organisms the critical variable is the amount and nature of the food available via Gibbs free energy, but it is not obvious that increased biomass should necessarily generate higher species diversity rather than greater abundance [26].

The biological mechanisms underpinning latitudinal diversity gradients remain a contentious issue. Several recent studies have evaluated a range of proposed historical, ecological and evolutionary explanations for latitudinal diversity patterns [4,11] and the species–energy relationship [8] (Table 1). Historical hypotheses largely focus on the older age of tropical regions and their greater age because of the late Cenozoic glaciations, but the persistence of latitudinal gradients through much of the Phanerozoic deprives these models of any generality. Most ecological models focus on higher productivity in the tropics, while evolutionary models invoke higher evolutionary or speciation rates, or lower extinction rates as an explanation for greater tropical diversity. It is difficult to unambiguously discriminate between these explanations, and it is likely that several factors are important. The better supported ecological hypotheses

Table 1. Mechanisms promoting positive species–energy relationships.

Mechanism	Rationale
Sampling	Ecological samples are more likely to sample more species in high-energy areas because the regional species pool is larger.
Population size	**Areas with more energy can support more individuals; species can maintain larger population sizes, reducing extinction risk and increasing species richness.**
Dynamic equilibrium	Greater energy increases resilience to disturbance, reducing vulnerability to extinction.
Niche position	**Greater energy increases relatively rare resources, allowing larger populations of species that specialize on these resources, decreasing extinction rate and increasing species richness.**
Niche breadth	Increased energy increases resource abundance, reducing niche breadth and overlap with adjacent species; species richness increases with less competitive exclusion.
Metabolic scope	**Greater energy increases the differential between resting and maximum metabolic rate, increasing the number of metabolic niches, and species richness.**
Trophic levels	Increased energy availability allows the introduction of additional trophic levels, increasing species richness.
Consumer pressure	As an ancillary to other mechanisms listed, consumer abundance/diversity is greater in high-energy areas. This reduces prey populations, limiting competition and allowing greater species richness.
Range limitation	Greater solar energy increases climatic conditions that are within the optimal range for more species, increasing species richness.
Diversification rate	**Increased energy generates faster speciation rates and/or lower extinction rates.**
Niche construction	Greater energy allows increased investment in niche construction activities, increasing abundance and reducing extinction rates, and increasing species richness.

The summary of mechanisms promoting positive species–energy relationships is based primarily on [8]. Mechanisms in bold have considerable empirical support; the possible role of niche construction is new and has not yet been rigorously investigated.

include: increased population size and thus increased extinction resistance, and an increase in species exploiting specialized niches as a result of greater amounts of energy available. However, there was no clear evidence that seasonality or long-term environmental stability was responsible for the species–energy relationship, contradicting suggestions [28] that climatic variability produced generalist species with broad geographic range (see also [26]). Temperature has been invoked directly in the 'metabolic niche hypothesis', which is based on the observation that metabolic rate for ectotherms increases with temperature, but the maximum rate increases more rapidly (greater metabolic scope). Consequently, at higher temperatures there is a greater variety of energetically feasible ways of making a living, or metabolic niches [26]. Over evolutionary time, it follows that the metabolic diversity of ecosystems may also rise and fall with temperature, and with the steepness of latitudinal temperature gradients.

Both historical and evolutionary models have been favored by recent studies of bivalves [29,30] and beetles [31], among other groups, which have established that

tropical diversity reflects the greater antiquity of the tropics, and their greater rates of diversification: the tropics are both 'the museum and the cradle' of diversity. Studies of the marine fossil record have demonstrated that this heightened tropical diversification rate involves both increased speciation [29,32], and a greater origination of new orders [33]; similar patterns have been reported in other clades [34]. Although some continue to advocate a role for the area of the tropics as a driver of diversity [35], neither age nor area can be a complete explanation for the pattern as they have varied considerably over geologic time; an integrated measure of area over time has shown some promise for understanding tropical forest diversity [36].

Evolutionary processes have been invoked in a variety of distinct models. The 'evolutionary rates hypothesis' suggests that higher temperatures increase mutation rates, possibly speciation rates, and the pace of evolutionary change [37–39]. For example, in a comparative study of closely related plant species, the rate of molecular evolution was twice as high in tropical species as in temperate congeners [40]. In contrast to the fossil studies cited above and other studies [32,41], this result was not due to faster speciation rates in the tropics. An evaluation of this hypothesis concluded that while there was evidence for a link between higher energy levels and increased mutation rates, there was far less evidence that this translated to increased speciation [42], although, as noted above, speciation rates in the tropics are higher than in extra-tropical environments. Advocates of the metabolic theory of ecology [43] have extended the evolutionary rates hypothesis, and results from scaling theory, to support a model in which the distribution of resources within organisms follows a hierarchically branching, space-filling model, metabolic capacity is maximized, and the rate co-efficient is $\frac{3}{4}$. This model is highly controversial [42,44–47], and while rates of molecular evolution and speciation may be higher in the tropics, the utility of the metabolic theory of ecology in explaining the pattern is doubtful. This lack of support in ecological timescales [8] between diversity and environmental stability is consistent with fossil evidence [48,49] against the 'turnover-pulse hypothesis' (in evolutionary time) positing that climatic instability drives pulses of speciation [50].

Two additional hypotheses each involve an element of positive feedback that may increase tropical diversity. Dobzhansky [51] suggested that biotic interactions played a greater role in the tropics than in temperate regions, a concept expanded by Schemske [52], who has argued that the more constant flux of biotic interactions in the tropics drives a pattern of ecological adaptation, reciprocal speciation and coevolution. There is at least plausible evidence that biotic interactions are more important in the tropics, and that this may enhance speciation rates, and the diversity of species within regional ecosystems.

The second possibility is that niche construction, or the production of extended phenotypes that enhance the fitness of the population, may be greater in tropical regions. Niche construction includes a variety of activities, such as building nests or other objects that persist in the environment beyond the lifetime of the individual that constructed them [53,54]. The niche constructing activities of organisms require energy, and there may be greater available energy to expend on such activities in high-energy settings. This proposal is consistent with a study of 130 coral reefs that found diversity is closely associated with mean annual ocean temperature

and regional coral biomass [55]. Niche construction appears to have increased through the Phanerozoic [56] and the relationships between species diversification, niche construction and climate deserve further exploration.

Despite the fact that multiple processes appear to be involved in generating tropical diversity, enough is known to allow us to establish some first principles of the relationship that we might expect between climate, evolution and diversity over evolutionary time scales. Within a geographic and climatic regime, evidence to date suggests that the primary factors responsible for diversification of specific clades are population size, metabolic scope and niche position; biotic interactions and niche-constructing ability might also be significant. Studies on both recent and fossil groups also reveal that diversification rates are higher in the tropics (high-energy) than in extra-tropical environments, although the causes remain unclear. Establishing first-order expectations requires knowledge of the climatic state of the Earth, the changing positions of the continents and the amount of area in the tropical regions, and, for marine organisms, the extent of shallow continental seas, particularly in tropical regions (hypsometry) [57–59]. Continental movements have altered the relative distribution of continents through the Phanerozoic, and changing sea level has caused the waxing and waning of broad, epicontinental seaways. During the Cretaceous, 100 Ma, high sea levels formed wide, tropical epicontinental seas in North and South America, northern Africa and southern Europe. Moreover, the broad Tethyan embayment allowed formation of a circum-equatorial current and very different current patterns and latitudinal distribution of heat from today. Yet tropical continental shelf area was far greater in the Paleozoic, and has declined since the Cambrian with a corresponding decline in the area of shallow-water carbonates [60,61] (Figure 1). Most of this decline occurred during the late Paleozoic; Early Cretaceous tropical shelves were the most extensive of the post-Paleozoic, but they were still less extensive than any time before the mid-Carboniferous.

Ceteris paribus, we should expect the greatest diversification during globally warm intervals with dispersed continents and broad shelves, where migration out of the tropics is facilitated, and perhaps with only moderately continental seas. Paradoxically, extensive epicontinental seas in tropical regions during greenhouse periods might have less diversity than during more moderate conditions because of the reduced oxygenation of the waters and difficulty of exchange with open marine settings [59]. We can now attempt to relate these principles to the empirical fossil record.

Climate and Global Marine Diversity

Testing first-order relationships between Phanerozoic marine diversity and climate should be relatively easy: compare global Phanerozoic diversity patterns to the record of climate, and note the effects of pronounced climatic shifts on biodiversity, rates of speciation and evolutionary innovation, episodes of pronounced declines in diversity and other relationships. Although geologists and paleoclimatologists have produced at least a first-order climate record for the past 600 million years there is far less agreement among paleobiologists about the record of marine diversity (Figure 2).

The fossil record of species is too sparse to be a reliable metric of global diversity, so paleontologists have instead relied upon compilations of more inclusive taxonomic

Figure 2. Phanerozoic marine diversity.

The number of marine genera is plotted against time. Sepkoski's marine generic data (brown) are based on first and last occurrences of both vertebrates and invertebrates. The Paleodatabase project data (blue and green; raw SIB and three-timer correction; from [6]) are based on a standardized sampling of a large dataset of occurrences of marine animals (excluding tetrapods) at specific localities for 48 temporal bins of roughly equivalent duration, and is corrected for various sampling problems, particularly by removing fossils from unlithified sediments. Raw SIB: raw sampled in bin diversity; three-timer correction: a smoothed version of raw SIB. All three curves have been rescaled against the maximum diversity to allow comparison between them. The distribution of glacial periods (light blue) is shown above the time line. Sepkoski data from [75], corrected for the revised geological timescale and the bins used in [35]; Paleodatabase data courtesy of John Alroy. (C: Cambrian; O: Ordovician; S: Silurian; D: Devonian; C: Carboniferous; P: Permian; Tr: Triassic; J: Jurassic; K: Cretaceous; T: Tertiary.)
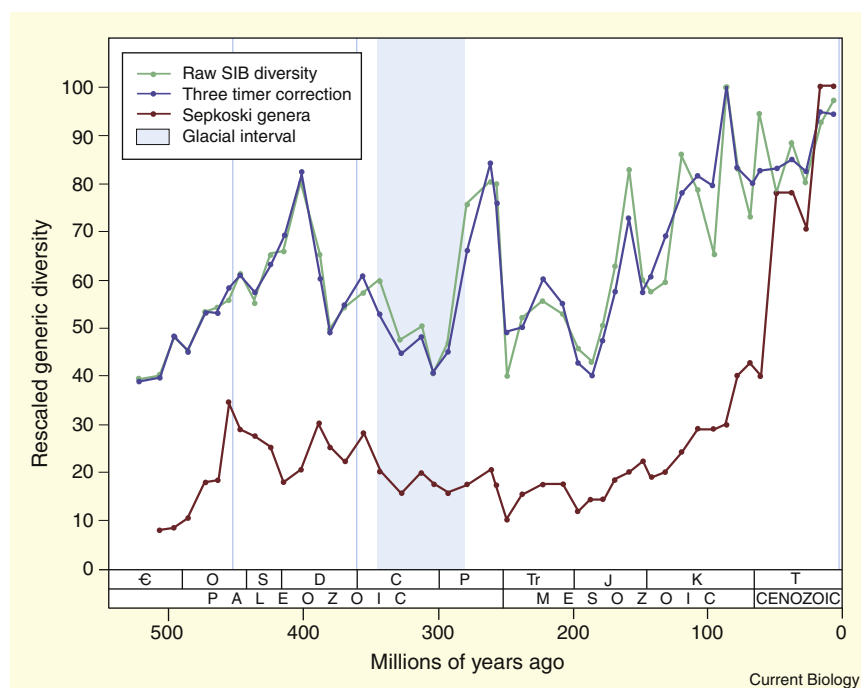
entities, primarily families and genera. Sepkoski's [62–64] classic compendium of the first and last occurrence of Phanerozoic marine families and genera exhibits a very strong post-Cretaceous increase in diversity, matching earlier expectations [65] from the increased latitudinal thermal gradient through the Cenozoic (Figure 2). Although this view of an almost exponential increase in diversity over the past 100 million years or so was widely accepted within the paleontological community, other views have persisted. Sepkoski [62] proposed a three-phase logistic growth model of Phanerozoic diversity in which diversity was constrained rather than unbounded, and thus he seems to have viewed the post-Paleozoic diversity increase as additive rather than exponential (John Alroy, personal communication 2008). Raup [66,67] argued that this diversity pattern was largely an artifact of the increasing volume of younger rocks. Recent quantitative studies of the distribution of sedimentary deposits through the Phanerozoic have verified Raup's [66,67] concerns and established that apparent records of Phanerozoic marine diversity as measured by Sepkoski and others are biased [68–73], although the magnitude of the bias on diversity estimates remains disputed.

As a consequence of these concerns, a new compilation of Phanerozoic marine generic diversity has been assembled by the Paleobiology Database Project (http://paleodb.org) with sample-standardization and other approaches applied to correct for potential bias [6]. This produces a much different view of Phanerozoic diversity than the canonical Sepkoski curve (Figure 2). Instead of a substantial Cenozoic increase, diversity increases only by a factor of 1.5–1.8 compared to mean Paleozoic levels. Moreover, there is a previously unrecognized Jurassic increase in diversity, and a strikingly different pattern of Paleozoic diversity. Although this is not the forum to dissect the reasons for these different curves, a couple of points are important. The sample standardization and other corrections of the Paleobiology Database Project curve should, in principle, produce a more accurate depiction of diversity. However, the corrections include removal of specimens from unlithified sediments, which are overwhelmingly from the younger part of the rock record. There is little doubt that unlithified samples are generally easier to collect, and thus may have inflated diversity toward the recent. Some paleontologists are concerned, however, that the statistical approaches may have 'over-corrected' for this problem and thus dampened a real increase in Cenozoic diversity. In other words, this correction may have removed exactly the pattern of diversity change that is of interest. Moreover, decades of studies of the diversity in local assemblages suggest greater within community (α) diversity in Cenozoic communities relative to Paleozoic communities, and Cenozoic genera appear to have a greater number of species than do Paleozoic genera.

Paleontologists are now confronted by very different descriptions of Phanerozoic marine diversity, each with flaws. The Sepkoski dataset and a similar (although more problematic) data set [74] has been the basis for many studies, including a recent analysis of the correlation between Phanerozoic temperature (derived from low latitude sea surface oxygen isotope ratios [75]) and family and generic diversity. This analysis suggests high diversity as well as increased extinction and origination rates during warm intervals [76]. Increased diversity was apparently associated not with changes in climate, but with the long-term average temperatures. Interpreting these results is hampered by the problematic dataset as well as the emphasis on temperature and the failure to consider the changing distributions of tropical continental shelf area. In contrast, two recent studies compared the Cenozoic mammal record to climate change and found little evidence for an association [77,78]. The first-order considerations developed in the preceding section do not appear to coincide with the Sepkoski curve, but the correlations for the Paleobiology Database Project curve are more intriguing. Mean Paleozoic diversity is higher on the Paleobiology Database Project curve than some

expected, but this coincides with the extensive tropical shelf area of the Silurian and Devonian. Diversity dropped through the Carboniferous, coincident with the Permo-Carboniferous glaciation and global cooling, but rebounded in the Early Permian (a rebound not observed in the Sepkoski data) during an interval of warm, tropical inland seas, such as the Zechstein of northern Europe and the broad embayments of the southwestern United States and Texas. The increasing diversity through the Mesozoic occurs during an interval of generally warm global climates and moderate latitudinal temperature gradients. This gradual increase in diversity appears to have come to an end in the Cenozoic with the advent of a stronger latitudinal thermal gradient and cooler climates. There is, then, at least a rough correspondence between the Paleobiology Database Project (PDBP) diversity data and global climate patterns. A more focused effort on particular well-documented episodes of climate change and associated evolutionary effects may be more informative, however. The following section is not a comprehensive history of the relationship between past climate change and evolution, but focuses on some critical intervals that illuminate these issues.

Evolutionary Effects of Past Climate Change

The glaciations of the late Neoproterozoic were probably the most extensive glaciations of the past billion years, with evidence from paleomagnetics and sediments suggesting equatorial glaciers near sea level during both the Sturtian (about 750 Ma) and Marinoan glaciations (ending 635 Ma) [79–81]. Each event encompasses at least two glacial pulses (and quite possibly more). Both the extent and the cause of these glaciations remain highly controversial. Some geologists have proposed alternative explanations to so-called 'snowball Earth' glaciations. It is worth noting, however, that equatorial ice at sea level virtually requires a frozen Earth, although it may have been a 'slushball' rather than a hard snowball, and the highly unusual cap carbonates found immediately overlying many of these glacial events require very unusual ocean chemistry. So, almost any explanation for these events is going to be far outside our more recent understanding of climate. As the first evidence of animals, in the form of sponge biomarkers, is found after the Marinoan (635 Ma) glaciation [82], and the earliest soft-bodied Ediacaran fossils appear soon after a brief glaciation at 580 Ma, it has been suggested that the glaciations triggered the early origin and diversification of animals [80,83,84]. There is, however, no evidence for an evolutionary response among the microbiota [85]. Climatic change is an implausible trigger for the extensive developmental and ecological innovations associated with the Cambrian radiation [86], but a more plausible case can be made that the aftermath of these glaciations helped oxygenate the oceans, which seems to have been a prerequisite for evolution of complex animals [87,88]. While this is an area of active and contentious research, the abiotic effects of climate change may have altered the environment in a direction favorable for the early diversification of animals.

The three best studied of the five great mass extinctions of the Phanerozoic were each associated with sharp changes in climate: the end-Ordovician (443 Ma) with a brief glaciation, and the end-Permian (252 Ma) and the end-Cretaceous (65.5 Ma) with global warming. The end-Ordovician extinction truncated the Ordovician biodiversification event. It occurred in two phases, perhaps a million years apart, with the first phase corresponding to the onset of glaciation and the second phase a waning of the ice age. The environmental consequences of these events included major shifts in stable isotopes, a temperature drop of perhaps 10°C, changes in nutrient cycling and a significant drop in sea level [89]. Endemic marine clades experienced higher extinction than cosmopolitan ones, as the number of marine biotic provinces declined [90]. One of the conundrums of this event is how a glaciation evidently no greater than that of the Pleistocene (in terms of the extent of ice coverage) could have generated one of the most extensive mass extinctions. The explanation probably lies in the sudden onset of the event and the loss of widespread continental seas.

The end-Permian event was the most extensive mass extinction of the Phanerozoic, with upwards of 80% of marine genera disappearing and substantial losses of plants, insects and terrestrial vertebrates, all over less than 300,000 years [91]. The extinction coincides with the eruption of a massive continental flood basalt covering much of Siberia with several kilometers of basalt. In addition to the CO_2 and sulfates released by the volcanism, excursions in carbon isotopes demonstrate a substantial volume of carbon from other sources was also released. The net effect was the rapid onset of a greenhouse effect in the Early Triassic, exacerbating the extinction and perhaps prolonging the recovery [91–93]. An extra-terrestrial impact brought the Cretaceous to a close with a sharp, brief cold spell caused by the cloud of dust and debris, followed by an interval of global warming [94]. In each of these three mass extinctions, rapid climatic changes are associated with massive losses of biodiversity.

In contrast to the brief end-Ordovician glaciation, a prolonged cooling period and extensive glaciations developed in the Carboniferous and Early Permian, an interval of perhaps 90 million years. Although geologists have tended to view this as a geographically extensive and volumetrically massive, long-lasting glaciation, the cyclically deposited marine sediments suggest a more dynamic pattern with frequent transitions between glaciated and ice-free conditions [95]. Changing levels of carbon dioxide appear to have been the primary driver for these fluctuations [96]. On land, these changes in CO_2 levels were likely responsible for the increasing dominance of conifers and other plants adapted to cool-dry conditions. A significant mass extinction of marine organisms (28% of marine genera) coincided with the onset of the glaciations, particularly among species with a narrow geographic range [97]. The more interesting pattern, however, was a persistent interval of low evolutionary turnover in the oceans after the onset of glaciation, with reduced species origination and extinction until the end of the glaciations in the Early Permian [97–99]. This 50 Ma interval of sluggish evolution appears to have favored generalist taxa with large populations, and broad dispersal, conditions which tend to depress originations and extinctions [99]. For example, in a global study, brachiopods with narrow geographic ranges, predominantly found in the tropical regions, experienced heightened extinction and diversification in the tropics after the end of the glaciation [98,100], although a more regional analysis found increased eurytopy but no heightened extinction of taxa with narrow geographic ranges [101]. These patterns are consistent with expectations from the analysis of species–energy hypotheses described above, and particularly with the 'metabolic scope hypothesis' [8].

A very rapid interval of global warming 55 million years ago is associated with biotic responses among the terrestrial

biota. This Paleocene-Eocene thermal maximum involved rapid warming over 20,000 years, followed by a 100,000 year greenhouse interval with a 4–5°C mid-latitude terrestrial temperature increase, perhaps because of the release of a large volume of methane [102]. A phylogenetically disparate array of new mammalian orders first appeared at this time, including artiodactyls, perissodactyls and primates. Correlation via an excursion in carbon isotopes shows that these first appearances all occurred within 10,000 years of each other in North America, Europe and Asia. The diversity and frequency of insect herbivory on leaves in Wyoming underwent a significant, transient increase during this thermal spike, probably associated with the movement of tropical insects into higher latitudes [103]. Plant communities in Wyoming also reveal an influx of more thermophilic species at this time [104].

Climate, Evolution and Innovation

Most biologists and geologists have a general sense that climate and climate change have played a significant role in the history of life. Confirming this suspicion and identifying the mechanistic basis of the relationship proves to be much more difficult. In many cases the impact of climate is indirect, through abiotic changes in weathering rates, circulation patterns, and similar effects. The three best-studied mass extinction events are associated with sharp changes in climate and support the contention that rapid shifts in climate can reduce global diversity. The long interval of stagnant evolution during the Permo-Carboniferous glaciation is consistent with studies of modern-day latitudinal diversity that rates of evolutionary innovation and diversification are higher in high-energy climates than in low energy climates. In general, contemporary studies suggest a positive relationship between high-energy climates and increased diversification rates, increased number of niches because of increased metabolic scope, and more specialized niches, and possibly because of niche construction. Studies showing that the tropics are a cradle of diversity, pumping clade representatives into higher latitudes, as well as evidence of increased ordinal level originations in the tropics, and of the sudden appearance of several mammalian groups during the Paleocene-Eocene Thermal Maximum suggest an asymmetric pattern of innovations associated with high-energy climate regimes. There is an intriguing possibility that diversity does not track climate, but rather builds up during warm intervals but without falling by proportional amounts when climates turn cooler. Thus, warmer climates may serve as an evolutionary diversification pump with higher diversity persisting, at least for a time.

Establishing a general relationship between diversity and climate through the Phanerozoic continues to be hampered by controversy over patterns of marine diversity. Examining more constrained time intervals may be more profitable, but can often be hampered by difficulties in correlation and uncertainties in temporal resolution. As high-resolution dating techniques spread [105], they should produce more robust systems for relating climate and diversity.

Acknowledgements

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