Biodiversity in space and time - insights from the fossil record

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One-sentence summary: Understanding geographic variation in deep time biodiversity is central to addressing the incompleteness of the fossil record and can provide important insights into biogeographic patterns and macroevolutionary processes.

Abstract. The fossil record is the primary source of insight on how biodiversity has varied in deep time, providing unique information on the long-term dynamics of diversification and their drivers. However, interpretations of fossil record diversity patterns have been much debated, with a traditional focus on global diversity through time. Problems arise because the fossil record is spatially and temporally patchy, and so-called 'global' diversity estimates actually represent the summed diversity across a set of geographically- and environmentally-distinct regions that vary substantially in number and identity through time. Furthermore, a focus on global diversity lumps the signal of ecological drivers at local- and regional-scales with that from global-scale factors that cause variation in provincialism and the distribution of environments; and cannot be untangled by studying global diversity curves alone. These conceptual and empirical concerns necessitate a shift away from the study of 'diversity through time' and towards the study of 'diversity across time and space'. Spatially-explicit investigations, including analysis of local- and regional-scale datasets, are central to this goal and allow analysis of geographic scale, location (e.g. paleolatitude), and the environmental parameters directly experienced by organisms. Studies so far have shed light on the stability of species richness variation among environments through time, and the poten-

tial climatic and Earth system drivers of changing biodiversity. Ultimately, this research program promises to address key questions regarding the assembly of biodiversity, and the contributions of local-, regional- and global-scale processes to variation in diversity through time.

Introduction.

Earth's biosphere hosts many millions of species today, resulting from 4.5 billion years of evolution and extinction since the origin of life[1]. Understanding the long-term pattern of diversification that gave rise to this biodiversity, and its drivers, is a central goal of evolutionary research that has been addressed primarily by paleobiology — the study of the fossil record (e.g. refs[2–6]). For decades, paleobiologists have emphasized 'diversity through time' at the largest spatial scales (e.g. refs[2,4,7–10]), primarily focusing on long-term changes in the total number of species on Earth or proxies thereof (but see e.g. refs[3,11–14]). Long-standing controversies have centered on whether diversity has increased exponentially (or 'essentially exponentially'[15–17]) or was characterized by long intervals of stationary dynamics, punctuated by abrupt diversity increases, which has been taken as evidence for diversity-dependent or logistic diversification (e.g. refs[2,4,18]).

This uncertainty regarding first-order patterns of biodiversity has fueled debates about the underlying processes and drivers of diversification, including questions of whether diversification is bounded or unbounded[19,20], the influence of abiotic factors versus among-species interactions (e.g. refs[21–25]), and the roles of mass extinction events (e.g. refs[2,4,17]). Nevertheless, there is little doubt that biodiversity has varied enormously through time, and most likely is more speciose today than it was 600 million years ago (before the diversification of bilaterian animals) or even 150 million years ago (before the diversification of flowering plants; e.g. ref[12,26]).

Biodiversity also shows tremendous spatial and environmental variation at any given moment in time. This spatial variation has been evident since the earliest natural history surveys[27] and is the cornerstone of biogeography and macroecology. Several first-order patterns are well-established and have remarkable generality. For example, (i) biodiversity is regionalized, with substantial turnover of species and groups across space and among environments (provincialism[14,28]); (ii) a large fraction of biodiversity is hosted in just a small number of environments, including reefs in the marine setting and geographically-widespread tropical rainforests on land[29,30]; (iii) biodiversity is generally high in the tropics and decreases towards temperate and polar latitudes (the latitudinal biodiversity gradient[29,31,32]); and (iv) larger geographic areas are generally characterized by higher biodiversity than smaller areas, a phenomenon referred to as the species-area relationship[33,34]. This spatial variation in diversity holds clues about the underlying process of diversification because the processes that cause biodiversity to vary across space are most likely related, either directly or indirectly, to the drivers of biodiversity through time.

Biogeography has provided important observations and theory relevant to interpreting patterns of diversity in the fossil record. One of the most fundamental of these is that diversity is regulated by a dynamic balance between the rate of new species appearing in a region, either through immigration or speciation, and the extinction of species already present[35] (used in paleobiology by e.g. refs[4,18]). Paleobiology has also provided insights into how biogeographic patterns seen today have varied in deep time, including the latitudinal biodiversity gradient (e.g. refs[31,36,37]) and species-area relationships[38–40]. However, compared to the long-standing focus on interpreting diversity through time at global scales (e.g. refs[2,4,10,15,41–43]), relatively few studies have investigated spatial or environmental variation in diversity or diversification using fossil evidence, in spite of its clear importance[14,21,38,44–49]. Indeed, spatial variation in diversity at any given moment in time may even be greater than temporal variation throughout most of the Phanerozoic fossil record of marine animals[50]. Therefore, unless spatial variation in sampling is explicitly addressed during analysis, most of the apparent variation in richness through time could simply reflect latitudinal, environmental or other secular biases in the spatial distribution of fossil localities through time. These biases would give rise to apparent trends in biodiversity, even if global richness was invariant, suggesting that variation through time cannot be understood separately from variation in space. However, spatial variation is as-yet poorly characterized or explained.

We advocate a shift in thinking from ‘diversity through time’ to ‘diversity across time and space’. This conceptual shift can shed light on the origins and drivers of major biogeographic patterns seen on Earth today. It may also be fundamental to resolving important debates at the heart of paleobiology regarding how biodiversity has varied through deep time, and the drivers of this variation. To achieve this conceptual shift, formal and widespread integration of spatial and environmental information is an essential next step in the development of paleobiology. We explain why a focus on estimating and interpreting "global" biodiversity through time has been misleading from both a conceptual and an empirical perspective — not least because the fossil record itself is not truly global in scope. Even if the rock record was global in scope, it would still be difficult to interpret drivers of biodiversity change based on global patterns alone, because they combine the signals of local- to regional-scale processes (involving environmental and among-species interactions) with those of global scale controls (such as provinciality and the distribution of species-rich environments).

In spite of its limitations, the fossil record is likely the only informative archive of long-term variation in Earth's biodiversity[51]. This is especially true given that recent literature has demonstrated grave problems with estimates of diversification rates from molecular phylogenies[52,53]. Despite early optimism about the estimation of extinction and net diversification from phylogenies of extant species along[54], it is increasingly clear that the assumptions encoded in the statistical inference machinery are violated by real datasets and yield unreliable estimates in practice[53,55–57]. Integrating fossil evidence into biodiversity studies is therefore a pressing concern for macroevolution. Analyses of biodiversity, however, must explicitly accommodate the empirical and conceptual problems associated with spatial sampling and geographic scale described here. We illustrate how spatially-explicit analyses of the fossil record can circumvent these problems and advance understanding of the fundamental macroecological and biogeographic patterns of extant biodiversity, as well as the times of origin and underlying causes of these patterns.

The meaning of fossil record diversity.

Diversity in the fossil record has been quantified using numerous metrics, including counts of species or higher-level taxa (taxonomic diversity or richness), ecological diversity[58,59], and morphological diversity (disparity[60]). However, study of taxonomic diversity has been the most common and is our focus here. Species in the fossil record are 'morphospecies', delimited using morphological characteristics. They therefore have an imperfect equivalency with the biological species concept based on reproductive isolation[61]. Although imperfect, delimitation of morphospecies has been shown to have close congruence with molecular delimitation in some groups (e.g. Foraminifera[62]; cheilostome bryozoa[63]) and provides our only source of information on the rich array of life that has existed on Earth. Moreover, large numbers of extant species are likely defined on morphological grounds, with little attention to reproductive isolation in practice (e.g. ref[64]).

Paleontological diversity patterns have often been quantified using counts of higher taxa, including orders[8], families[4,15], or genera in recent studies (e.g. refs[2,7]). Genera are used, either explicitly or implicitly, as proxies for relative variation in species richness because genera are considered easier to diagnose and recognise than fossil species[65], show greater taxonomic stability, and because sampling must be more complete for higher taxa than for species (e.g. ref[9]). However, the use of genera as proxies for species is not without issue, since higher taxa may not reflect species-level diversity patterns[66].

‘Global’ diversity through time — four decades of research.

Paleontologists have been interested in patterns of diversity through time almost since the birth of the geological sciences[5]. Paleontological ‘diversity through time’ is typically synonymous with global-scale patterns, and debates over the macroevolutionary processes of diversification in particular have been dominated by discussion of global diversity curves (e.g. refs[2,4,15,18]; but see refs[3,12,14]). We recognize two broad approaches to characterizing global diversity through time — face value interpretations of global diversity, and sampling-standardized interpretation of global diversity.

Face-value interpretations of global diversity through time. Face-value counts of taxa through time take the fossil record as a literal documentation of variation in diversity through time, without attempting to correct for variable sampling. These counts suggest that marine animal diversity has tended to increase through time (e.g. refs[5,15,67]), punctuated by abrupt decreases during rare mass extinction events that also caused significant turnover at a high taxonomic level (e.g. ref[68]; Fig. 1A). The apparent trend of increasing diversity is most prominent during the past 100 million years, suggesting that marine animal diversity may be much greater today than at any time in the geological past. This trend is least prominent during the ‘Paleozoic plateau’, an interval of stationary dynamics spanning around 200 million years from the Late Ordovician to the late Permian[4] (Fig. 1A). The implications of this face-value, global pattern for understanding the drivers of biodiversity have been intensely debated, with the same curve seeming to support both diversity-dependent and diversity-independent (or 'exponential') interpretations[4,15,17]. Global-scale, face-value studies of land vertebrate families[69] (Fig. 1D), insects[70], and land plants[26] have been also interpreted by some authors as providing strong evidence for exponential diversification on land (e.g. ref[16]).

Direct interpretation of face-value, 'global' curves as a record of diversity through time either assumes: (1) That sampling is relatively complete; or (2) That fossil preservation, recovery, geographic representation, and reporting do not vary systematically through time (i.e. that it is relatively even or equivalent through time). These two assumptions were questioned even from the earliest phases of research[9]. Nevertheless, widespread consensus emerged in the early 1980s that any potential biases had small effects compared to the signal of diversity through time in the data[67], a conclusion that was supported by indirect evidence such as congruence among diversity curves of higher taxa from different datasets[67] and the apparent match between phylogenetic branching order and the temporal order of appearance of fossil groups[71]. This consensus remained relatively unquestioned until the early 2000s, when various studies called renewed attention to the problems posed by large-scale variation in rock amount or sampling intensity of the fossil record through time (e.g. refs[72–74]). Increasing evidence since then has undermined the usefulness of face-value taxon counts for study of large-scale patterns in many groups. The few exceptions so far are those groups that have been demonstrated to show high species-level sampling rates (Foraminifera[23], horses[75], graptolites[76]).

Estimating global diversity through time from fossil occurrence data. The late 1990s and early 2000s saw development and rise to maturity of the Paleobiology Database (paleobiodb.org), which records individual occurrences of fossil species within localities, aiming to provide a comprehensive account of the published fossil record. This and other large-scale fossil occurrence databases (e.g., Neotoma, Neptune, GBIF, iDigBio[77]) have accelerated the transition towards methods that quantify variation in sampling intensity (e.g. refs[78]) or use sampling-standardization to account for such variation (e.g. refs[2,7]). Key findings of sampling-standardized approaches include: (i) strengthened support for logistic or diversity-dependent diversification in marine animals at the 'global' scale, especially within higher taxonomic groups between mass extinction events[2,7] (and see refs[23,75,76] providing evidence of diversity-dependence in empirically well-sampled groups); (ii) that marine animal diversity today may not be much greater than it was during the mid-Devonian or mid-Permian[2,7] (Fig. 1A); and (iii) evidence for effects of environmental controls on species richness at large scales (e.g. in marine animals[2,7]; and see refs[23,75] for empirically well-sampled groups).

Sample standardization approaches have enabled a transition away from face-value counts of named fossil taxa towards statistical estimation of patterns of diversity and diversification in deep time (e.g. Fig. 1A). These methods include classical rarefaction and other approaches that draw equivalent counts of data items (e.g. occurrences of species within fossil localities) through time[79], coverage-based sample standardization methods such as shareholder-quorum subsampling (SQS) that draw data items up to equivalent coverage of the underlying taxon-occurrence frequency distribution[2,80], methods that estimate the diversity of common species[81], and methods that attempt to quantify and correct for sampling intensity based on numerical models (e.g. the 'TRiPS' method[82]). Various shortcomings are evident and further scrutiny may be required. For example, classical rarefaction smooths out diversity curves, removing genuine variation[2], and the TRiPS method often fails to extrapolate, instead (and incorrectly) tracking face-value richness[83,84]. PyRate, an approach that estimates sampling rate, origination and extinction[85], and includes diversity patterns in its outputs, is becoming more widely-used but may perform poorly except at high and relatively consistent levels of sampling density[86]. Coverage-based methods such as SQS are sensitive to variation in evenness[81,83], but may currently be among the best options.

In our view, controlling for variation in sampling intensity is an essential step in understanding the deep time record of biodiversity change. However, sampling standardization on its own does not control for variation the size of the "sampling universe"[38,39,47,49,83,87]; i.e. it does not control for factors that dictate the size or environmental scope of the fossil record itself. These factors include the geographic distribution and extent of the sampled fossil record (Fig. 1C, F), the differential sampling of environment types and paleolatitudes, variation in the preservation potential and representation of groups, and variation in research intensity (e.g. ref[49]). One clear illustration of this concerns crocodylomorphs (crocodylians and their extinct relatives), a species-poor, but ancient group of living reptiles. Regional-scale studies indicate that their low present-day diversity results from declines on all continents during global cooling and aridification of the past 35 million years[88]. However, global-scale analysis using PyRate returns a pattern of strongly-increasing diversity during the same interval[89]. This spurious pattern of increase is an artefact resulting from expanding the geographic scope of the fossil record to incorporate continents such as Africa, South America and Australasia that were poorly-sampled or absent from earlier intervals[88,90].

Global diversity can mislead about pattern and process

Attempting to connect "global" estimates of species richness to the underlying processes that regulate species richness is inherently problematic on both conceptual and empirical grounds (and see ref[91]). On conceptual grounds, global-scale diversity is the end result of a set of distinct processes operating across the entire hierarchy of spatial scales, so global curves are not informative about the processes that regulate species diversity within regions through time. For example, increases and decreases in global species richness could result from increases at local and regional scales under equilibrial dynamics influenced by the ecological interactions among species, or from increases in the number of biotically distinct regions due to global tectonic or climatic factors. There is no information in the global curve itself that allows discrimination between these alternatives (Fig. 2) or others; and note that the same concern applies to interpretation of global diversification inferred from molecular phylogenies. Therefore, the debate over process as inferred from global diversity through time curves (e.g., refs[2,4,15–17,22]) may be unresolvable, because global curves cannot distinguish between fundamentally different causal mechanisms that operate at different levels of the spatial hierarchy (Fig. 2).

On empirical grounds, the global focus is also problematic because the fossil record is not global in scope and varies considerably in the number and identities of geographic regions that are represented through time and among environments (Fig. 3). This imparts substantial bias onto notionally ‘global’ diversity curves (e.g. refs[44,46,49,50,90]). Biodiversity varies through several orders of magnitude among environments and regions on Earth today, and has done so for at least the past 500 million years (e.g. refs[3,47,50]). Left unquantified or unaccounted for, it seems obvious that this could cause misleading inferences of diversity patterns, thereby yielding spurious support for hypotheses of the diversification process and its drivers. Understanding what fossils might tell us about deep time patterns of diversity, therefore, requires understanding of the spatial, environmental and preservational structure of the fossil record.

Structure of the fossil record. Only a small fraction of species that have existed are preserved as fossils, and the resulting fossil record is incompletely sampled and studied. Preservational biases are evident at multiple scales. At local scales, the fossilization potential of individuals and species is influenced by numerous factors (e.g. refs[72,92]), affecting our understanding of ecological communities and local species richness[11,93]. For example, only 14% of fossil genera from the early Cambrian (~508 Ma) Burgess Shale would be present without the exceptional preservation of soft-bodied animals[94].

At larger scales, the fossil record in any one place has a patchy distribution through time[95], and the available fossil record of any given interval comprises some geographic regions that provide fossil evidence of the past biota, embedded in large regions for which no fossils are present (e.g. ref[49]; Fig. 3). Long-term trends are evident in the geographic distribution of fossil data. For example, younger sediments are more geographically widespread[49,50,90] (Fig. 1C, F) and are less lithified (i.e. softer) than older sediments, allowing an easier census of biodiversity[96,97]. Research effort, the extent to which paleontologists have explored, studied, and published on the available fossil record, also varies, ultimately affecting which data are recorded in databases. Nevertheless, the best-studied portions provide exceptional windows onto regional biotas of particular times and places in Earth history. These are not evenly distributed with respect to regions and environments, mostly representing North America and Europe[49], and notably deficient, so far, for tropical regions during the past 60 million years[44,46] (Fig. 4).

Species and groups are not equally represented in the fossil record, and neither are environments. Sedimentary basins, by definition, preserve rocks from topographically low-lying settings. This explains why the record is dominated by fossils from marine rocks. Many environments are almost never preserved in the fossil record (e.g. mountains and uplands), or are largely erased from the record over <10 million years ("doomed sediments", including cave and tar-pit deposits[98]). Skeletonizing marine animals are the traditional targets of fossil record diversity studies, but important data are also available for plants[12,26] (especially pollen and spores e.g. refs[99,100], land animals (e.g. refs[69,87,90,101]), and plankton (e.g. refs[23,102]) among others. The availability of these different study systems provides insights into biodiversity patterns across a wide range of environments for various, fundamentally different types of organisms.

The importance of variation in the geographic and environmental scope of the fossil record should not be underestimated. For example, 35–85% of variation in nominally 'global' diversity through time curves is explained just by the geographic spread of fossil assemblages[49,50,87,90] (Fig. 5). Therefore, rather than focusing on 'global' diversity, analyses should instead target local and regional diversity within well-studied windows in time and space that can provide the most reliable biodiversity estimates, controlling for variation in spatial scale. These well-sampled regional species pools, when analyzed in context of paleolatitude, local climate, and environment, may provide our best opportunity to understand the processes that have driven diversity through deep time (e.g. refs[3,11,50]).

A conceptual model for biodiversity across scales. Ultimately, species richness at a particular spatial scale is a function of speciation, extinction (or extirpation), and immigration: these are the only processes that can change the number of species within a particular geographic setting. Consideration of the scale at which different processes operate illustrates why global compilations can prove misleading about the drivers of biological diversity in both time and space. Variation in true global biodiversity through time can arise for reasons that are independent of the interactions among groups of species and their environments that influence speciation and extinction rates within biogeographic regions (Fig. 2). This decoupling can arise because global diversity is also a function of the truly global tectonic, climatic, and oceanographic processes that regulate the number of distinct biogeographic regions on Earth, and therefore the opportunities for allopatric divergence. All else being equal, species richness at the global scale can rise and fall with biogeographic regionalization, as implied by species-area relationships when splitting or lumping regional species pools[34]. Ironically therefore, global diversity compilations that ignore patterns at finer spatial scales are typically uninformative about truly global processes, because the effects of those processes are conflated with those of regional-scale processes (Fig. 2). We discuss three spatial scales of diversity and process in the fossil record – local, regional, and global – determined in part by the resolution and structure of the fossil record itself. The distinction between these spatial scales is inherently gradational, and the definitions of biogeographic regions may change with increasing evidence. Therefore, the descriptions below are intended as indicative and should not be taken as strict rules.

Local diversity. Local diversity is the assemblage of taxa associated with a particular fossil locality (e.g. a quarry), or set of time-equivalent localities within a small area. Local assemblages represent the set of individuals preserved within a single depositional environment (facies) within a rock unit, generally at the highest resolvable time resolution (e.g., a "bed"). This is the basis of most locality-taxon lists in the Paleobiology Database, and can be regarded as alpha diversity or community richness (e.g. refs[3,12,103,104]). Caution is needed when interpreting local diversity because the "death assemblage" of a fossil locality differs from a true ecological community; fossils can be transported in from adjacent areas, or time-averaged over hundreds or thousands of years, and many species from the in-life community may never be fossilized (e.g. refs[11,72,92,93]). Conversely, however, local assemblages may be free from biases caused by variation in the spatial or environmental scope of the fossil record[3] and therefore carry a coherent ecological signal that provides a strong test of how community-scale processes might regulate diversity.

Regional diversity. Regional diversity reflects the summed species richness across many local assemblages, and is dominated by evolutionary rates of speciation and extinction that occur within a particular biogeographic theatre. Regional or "biogeographic" scales are sufficiently large that allopatric speciation can occur, but sufficiently small that among-species interactions, together with the influence of abiotic factors, determine the shapes of the regional speciation, extinction, and immigration curves[35]. Operationally, 'regional' scales are identified in the fossil record by the set of fossil localities within a time interval at a defined spatial scale, such as a geological basin or continent. The hypothesis that paleogeographic areas represent coherent biogeographic regions can be tested using indices of faunal similarity among the fossil assemblages of localities, subregions or geological formations (e.g. ref[105]). Time resolution is limited by the precision of stratigraphic (dating) approaches, such that species should be considered as being near-contemporaneous, although in practice the time resolution may often be at the geological stage level, which approximates five million years in the marine fossil record. Finer stratigraphic resolution may be available for particularly well-sampled sections (e.g. in deep sea sediments; e.g. ref[23]), and a focus on local or regional scales rather than global may also allow improved stratigraphic resolution (e.g. ref[106]).

Crucially, regional and local scales can be characterized by the abiotic environmental factors actually experienced by organisms. These may be approximated using geological or geochemical data, or inferences from paleoclimate models as characterisations of the broad-scale regional environment (e.g. ref[107]). Moreover, regional and local assemblages are located in space, with definable geographic scale and (paleo)geographic locations. This information allows tests of the influence of regional environment on diversity, quantification of species-area relationships (e.g. ref[38]) or hierarchical beta diversity[40,108], and characterization of the latitudinal biodiversity gradient in deep time (e.g. ref[31]).

The regional scale can also be viewed as the maximum grain size that is typically useful for directly understanding how species richness varies as a function of the interactions between evolutionary diversification, immigration, community richness, and the abiotic environment. Regional rates of speciation, extinction, and immigration may be influenced by environmental variation, as well as the effects of biotic interactions among species and their food sources, predators, pathogens, and competitors[109]. These rates are often inferred as being dependent on regional species richness, a property referred to as diversity-dependence (in biogeography[35]; and paleobiology[8,21,110]. Diversity-dependence could result from the influence of biotic interactions on the architecture of species ranges, thus indirectly affecting the probabilities of lineage splitting and population persistence[8,111–113] (although correlations of range size with diversity and extinction rates are not evident on the coarse time-resolutions of typical fossil datasets[114]). Effects of biotic interactions on diversity trajectories therefore need not have anything to do with hypothetical carrying capacities or numbers of ecological niches at local-to-regional scales[115].

Global diversity. Global diversity represents the aggregate richness across all assemblages within a time interval. Importantly, most of the interactions among species, as well as those between species and the abiotic environment, occur within and not among biogeographic species pools. However, global scale diversity possesses one unique attribute that cannot be reduced to a lower level of the explanatory hierarchy: global richness may, in large part, be a function of the number of distinct biogeographic regions existing at any given time. We refer to this property of the global biota as global provincialism — the degree to which the Earth is subdivided into a set of more-or-less biogeographically coherent units (e.g. refs[14,34,43]).

Global provincialism can be influenced by a number of factors including the strength of latitudinal climate gradients[116], the degree of continental fragmentation and assembly[6,43], including mountain building on land[117,118], spatiotemporal heterogeneity of environmental conditions[32,119–121], and the distribution of different environment types. The extent of species-rich environments such as reefs and rainforests[3,122], and of species-poor environments such as epeiric seas, deep-shelf facies[47,48], and recently deglaciated landscapes may have particularly important effects on summed global biodiversity[14,21,122].

Spatially-explicit approaches to biodiversity in deep time

Regional-scale patterns. The effect of regional scale processes on diversity can be disentangled from global scale processes using spatially-explicit approaches, which are the focus of modern-day biogeography but have been less common in paleobiology. Paleobiological examples so far include studies that estimate diversity over an explicitly-specified spatial scale, such as local assemblages[3,12,103], regions of quantified size[38,39,50,90] or prescribed environmental or latitudinal scope[3,31,37,49], as well as regionally focused analyses in which the geographic scale of sampling is not explicitly quantified but does not vary substantially through time (e.g. the fossil record of New Zealand, North America, or the Iberian Peninsula[101,123–125]).

Studies so far indicate important effects of environment on local- and regional-diversity[3,50], similar to biogeographic patterns seen in the present day. Paleontological evidence that these associations also occurred in deep time include a consistent gradient of increasing diversity from stressed inshore habitats out to stable offshore habitats for local assemblages of marine invertebrates[3,11], and the occurrence of elevated richness in reefs throughout deep time[3,21,50,126]. Moreover, within-environment diversity levels show no evidence for long-term increases on timescales of tens to hundreds of millions of years (reefs[127]), or only very limited increases[3,11]. Large changes in diversity seem to have occurred infrequently, associated with the origins of major groups, such as during the Cambrian explosion; terrestrialization in plants, arthropods and vertebrates; origin of flowering plants and closed-canopy tropical forests and other events (see *Global-scale Processes*, below).

Studies of regional- and local-scale richness also generally show smaller amounts of variation in diversity through time than do ‘global’ studies. For example, this is true within major animal groups over long time intervals (>50 million years) in the marine fossil record, albeit with high variance around long-term averages (e.g. ref[50]; Fig. 1B). However, direct tests of diversity-dependence in regional assemblages have been difficult because of the patchy nature of the fossil record. Indeed, few datasets provide well-sampled, informative records of diversity and diversification rates within a single region over long time intervals, and fewer still have accounted for the effects of varying environments. So far, Cenozoic land mammals of North America provide some statistical evidence for diversity-dependent diversification rates[101] (and see ref[125] in Iberian land mammals). Land vertebrates in total also show stationary diversity at local and regional scales for much of the Mesozoic, and again (at a higher level) through the Cenozoic, with no evidence for increasing trends through time[39,87,103] (Fig. 1E). This pattern is consistent with diversity-dependent regulation at regional scales, which may also occur in regional paleofloras[12,112]. The global record of planktic Foraminifera has provided strong statistical evidence for a dynamic, climatically-mediated pattern of diversity-dependent diversification and effectively represents a ‘regional’ assemblage under the hypothesis that foraminifera represent a globally-distributed population[23]. Indeed, some of the clearest evidence for evolutionary processes driving biodiversity comes from open ocean sediments, possibly because ecological and environmental variation is less prominent and easier to control for.

Global-scale processes. The question of how many species have existed globally on Earth and how this number changed through time is clearly interesting. However, it may be impossible to estimate this directly, given the spatial incompleteness of the fossil record.

Therefore, we remain relatively uncertain about variation in global biodiversity and the relative contributions of different processes. Nevertheless, several factors have strong potential importance, including evolutionary innovation, and tectonic or climatic controls on global provinciality and the distribution of species-rich environments.

Evolutionary innovation and ecosystem restructuring. Evolutionary innovation in some groups may allow for increased diversity by accessing of new niches or ecospace, or by expanding available energy resources and allowing a step-change in diversity across spatial scales (e.g. refs[20,128,129]. This process can be considered 'global' because innovations can alter the energetic structure of the biosphere and influence dynamic feedbacks between species richness, speciation, and extinction. However, unlike other global processes, the effects of innovation should also be evident as an increase in diversity at local and regional scales. For example, large increases in local species richness for plant communities occurred with the origin of angiosperms[12] and may in part be explained by innovations in leaf venation that increased photosynthetic capacities[130], providing access to increased energy resources (e.g. ref[20]), with potentially-cascading effects for animal diversity[131]. Moreover, the diversification of bilaterian animal phyla at the start of the Phanerozoic almost certainly caused an increase in species richness in the oceans, facilitated by developmental innovations that enabled new ecologies such as burrowing and predation (e.g. ref[129]). Terrestrialization events among plants and animals have also clearly been important to the extent that biodiversity on land today is considerably greater than that in the oceans, despite the older origin of marine life (e.g. ref[132]).

Changes in taxonomic composition or ecosystem-restructuring due to extrinsic factors may also be important. For example, the shift from dinosaur- to mammal-dominated terrestrial ecosystems after the Cretaceous-Paleogene (KPg) mass extinction event induced large, abrupt increases of species richness at both local and regional scales on land[39,87,90,103] (Fig. 1E). A similar effect also occurred in marine environments with a step-wise, post-KPg increase in animal diversity, especially among gastropods[50] and probably teleost fishes[133]. It also triggered the origins of modern-type closed-canopy rainforests in the tropics[99]. These types of observations have been taken as evidence that ecosystem reorganization associated with mass extinctions can induce shifts in diversity equilibria, affecting diversity at all spatial scales[2,87,103].

Tectonic and climatic controls on global diversity. Global provinciality may be a major control on the sum of Earth's biodiversity[14,43,126], and its signature should only be evident at large spatial scales, unlike the other processes described above. Global provinciality is most likely regulated by tectonic factors such as mountain-building and continental fragmentation, as well as climatic and oceanographic variation[6,41]. For example, the strength of the global environmental gradient may correlate positively with provinciality, such that warm intervals may have shallow latitudinal climate gradients and therefore reduced provinciality, leading to lower global species richness[116]. However, the importance of any such decreases during warmer intervals compared to that of potential increases caused by widening of the geographic extent of species-rich environments is not known. Similarly, the relative importance of increasing species richness due to increased provinciality during cooler intervals, compared to decreases (at high latitudes) due to steepening of latitudinal biodiversity gradients (e.g. refs[31,37]) is not clear. This leaves unanswered questions about the net effect of variation in the environmental climate gradient on global biodiversity.

Empirical tests of the effects of tectonics and climate have so far been performed by studies that compared notionally 'global' diversity to variation in individual global Earth system proxies through time. Several distinct processes have been statistically associated with variation in 'global' diversity, including sea level and the extent of shallow marine area[41], sulfur- and carbon-cycling[41], global temperature[42] and continental fragmentation[43]. However, it is difficult to untangle the effects of many of these hypothesized environmental drivers, which are frequently collinear with each other[21] and with other Earth system and rock record variables. Therefore, although studies of this type have yielded important hypotheses of the drivers of global biodiversity, spatially-explicit studies may ultimately be required to test them further, potentially teasing apart the effects of linked Earth system drivers at nested spatial scales. These studies may include comparison of regional environmental variables to regional patterns of diversity or diversification within and across time periods (e.g. ref[125]) and quantification of species-area relationships and beta diversity at varying spatial scales as an approach to quantifying provinciality[40].

Patterns at increasing spatial scales — future prospects

We have said that it will be impossible to directly estimate total global biodiversity from fossil data, principally because the fossil record is not complete enough to give a direct estimate of global diversity in any of Earth's major environments (e.g. shallow marine, terrestrial) at any point in deep time. Nevertheless, paleobiology provides the only dataset that might allow us to put constraints on this important question, using information from exceptional, well-sampled but spatially- and temporally-restricted windows of the fossil record. These windows provide the best information on local, regional and environmental diversity levels, and how they vary in space (provinciality) (Fig. 3). Paradoxically, therefore, regional studies may hold the key to understanding global diversity variation in deep time.

Characterizing the effects of biodiversity processes across the hierarchy of geographic scales was first proposed during early stages of quantitative paleobiological investigation. Valentine et al[14] proposed a model specifying approximate regional diversity levels for biogeographic provinces, and the number of distinct provinces based on inferred latitudinal climate gradients and configuration of landmasses. Much has been learned since then, and an elaborated version of such a model, incorporating biodiversity processes across the full hierarchy of spatial scales, may ultimately address the question of variation in biodiversity through time. This early work[14] was closely followed by a widespread focus on 'global' diversity and climate indices that, while fruitful, has ultimately struggled to yield consensus on the drivers of long-term biodiversity change (e.g. refs[2,16,19,20]).

Efforts to advance knowledge of this topic will benefit from ongoing improvements in tectonic reconstructions of the Earth in deep time[134], global climate models for intervals of the distant past[135] and continued paleontological and stratigraphic study of well-sampled localities and regions. Field exploration could play a central role in advancing understanding of poorly-sampled spatial regions and environments, especially outside of Europe and North America[44,46,136]. A renewed focus on 'diversity across space and time' may ultimately answer some of the most central questions of paleobiology and macroevolution regarding the assembly of Earth's biosphere.

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Author contributions

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Competing Interests Statement

The authors declare no competing interests

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Figure captions

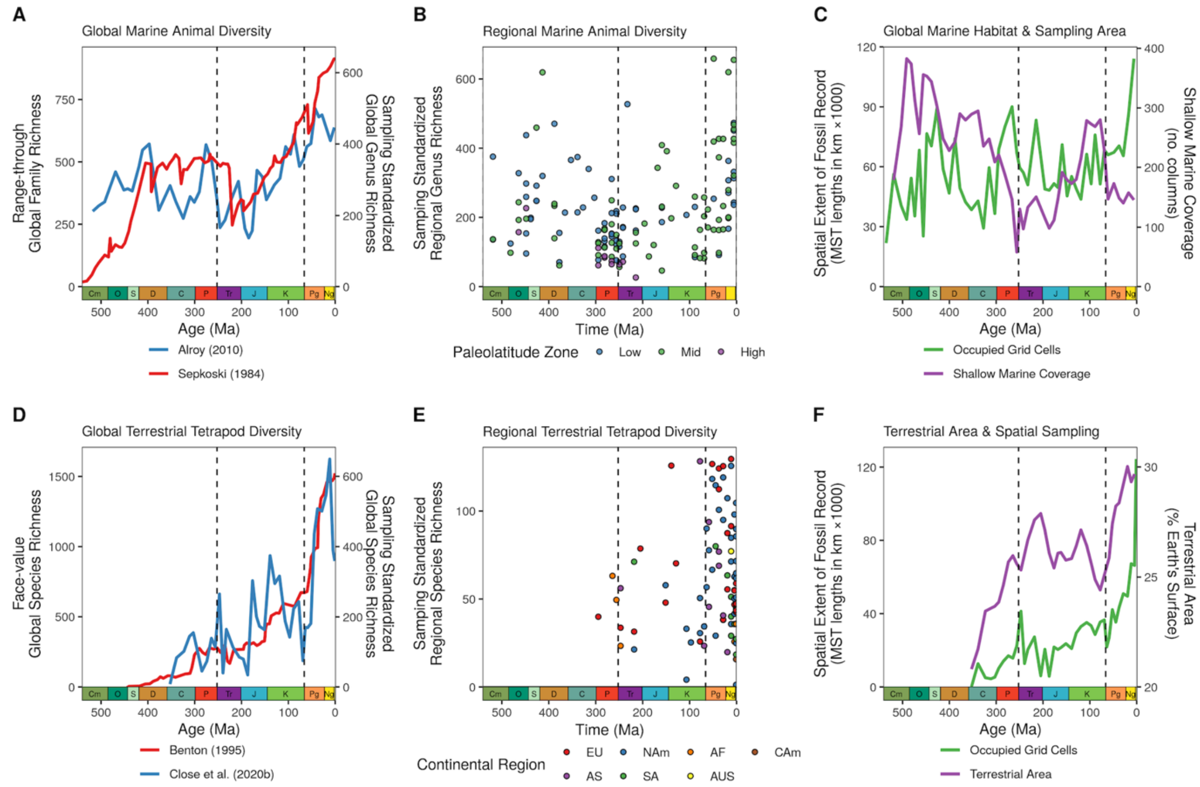

Figure 1. Global and regional diversity curves, fossil-record sampling, and ancient sea and land area. (A) Global marine diversity curves of face value (range-through; red)[4] and subsampled (blue)[2] genus richness. (B) Regional-scale subsampled marine animal diversity (Eumetazoa minus Tetrapoda) with a spatially-standardized scale of 2,500 km minimum spanning tree (MST) distance[50]. (C) Global marine area (purple) compared to sampled area (green) through time[50]. (D) Global land vertebrate diversity curves of face value family counts (red)[15] and subsampled species richness (blue)[90]. (E) Regional-scale sampling-standardized land vertebrate diversity, with a spatially-standardized scale of 2,500 km MST distance[90]. (F) Global land area (purple) compared to sampled area[90] showing lack of associated between the two.

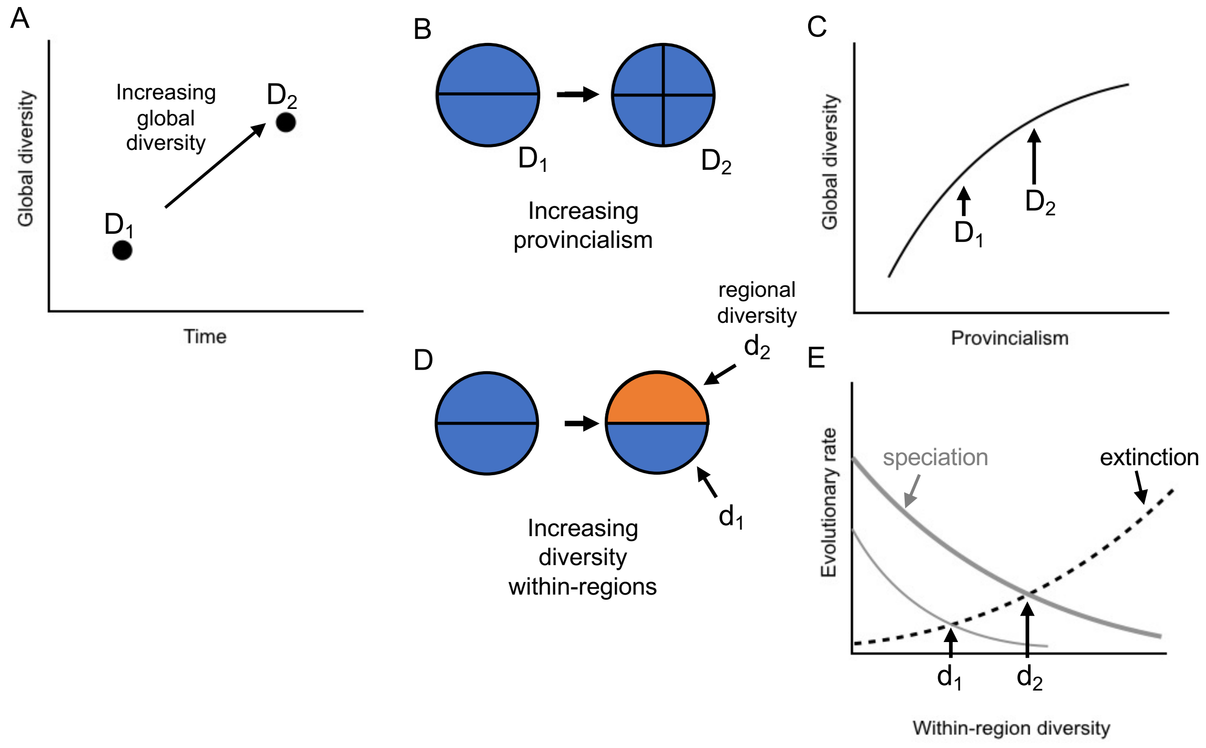

Figure 2. Increases in global diversity can result from different processes across the spatial hierarchy. For example, an increase in global diversity (A) can result from the splitting of large biogeographic province into smaller provinces (B), due to the expected positive relationship between provincialism and total species richness (C). Global increases can also result from increased diversity of individual regions (D), as might occur in an equilibrium model of regional diversity (E). In this example (E), the diversity of the orange region is increased relative to other regions because of an upwards shift in the relationship between speciation rate and regional diversity (solid gray line), yielding a higher equilibrium diversity (d_2) relative to other regions (d_1).

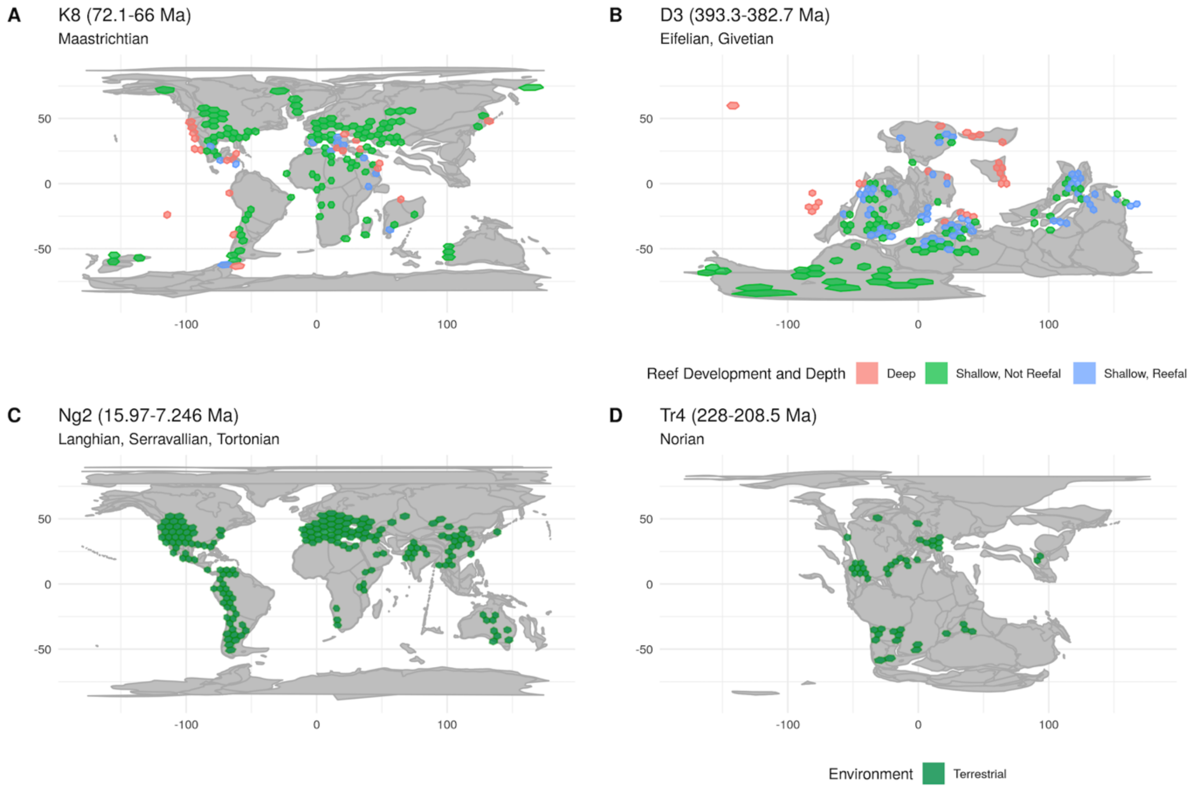

Figure 3. Paleomaps showing distributions of geographic and environmental sampling in the marine (A–B) and terrestrial (C–D) fossil records. (A–B) Distribution of marine animal fossil record and broad environmental categories for Maastrichtian and Eifelian–Givetian (Middle Devonian) intervals. (C–D) Distribution of terrestrial tetrapod fossil record for Langhian–Tortonian (Miocene) and Norian (Triassic) intervals. All panels use equal-area grid cells with 500 km spacings. Paleomaps plotted from C. Scotese's paleo digital-elevation models[137], fossil localities and environment classifications are from PaleoDB data reported in refs[50,90]

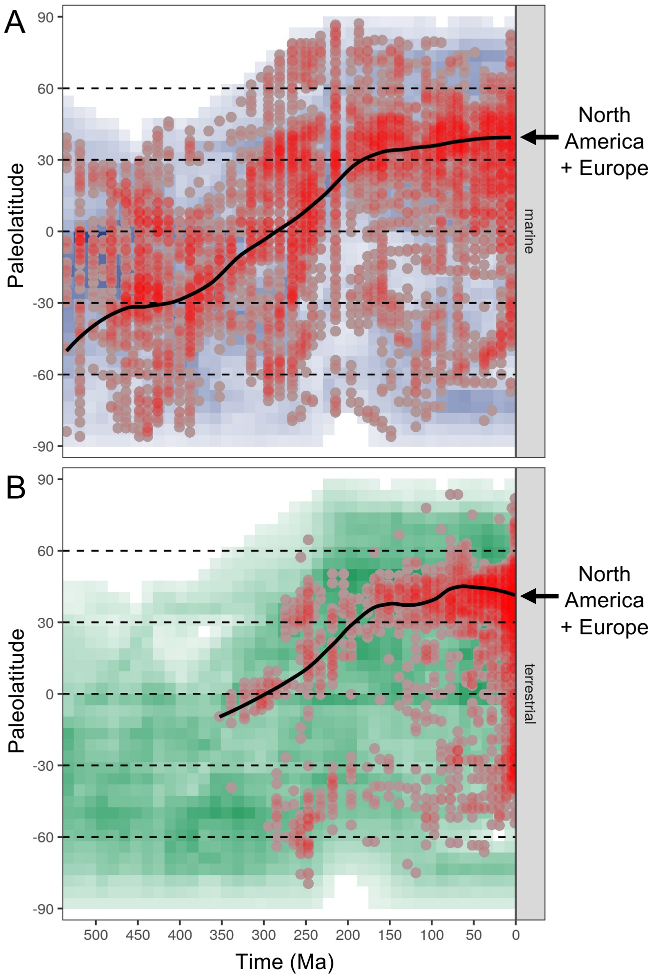

Figure 4. Paleolatitudinal distribution of fossil record sampling through time for Phanerozoic marine animals (A) and land vertebrates (B). Fossil localities are shown using red points on top of ancient shallow marine (blue) and land (green) areas estimated from C. Scotese's paleo digital-elevation models[137]. Black trend line follows paleolatitudinal centroid of North America and Europe showing concentration of most fossil record sampling on these continents[44,49].

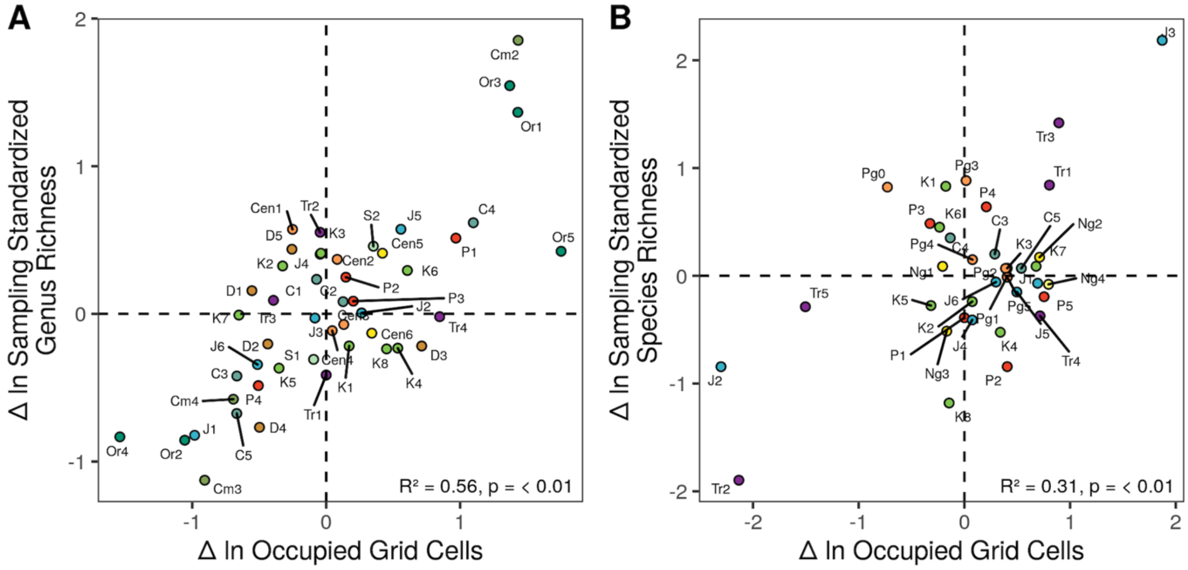

Figure 5. Correlation of "global" subsampled diversity with spatial extent of fossil record for marine animals[50] (A), and (B) terrestrial tetrapods[90]. First differences were used to correct for spurious time-series correlations and correlation statistics are based on Pearson's product-moment.