The future of the fossil record: Paleontology in the 21st century

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In the past two decades, great progress in the biological sciences has come from the incorporation of history in understanding basic mechanisms in fields ranging from ecology and conservation biology to physiology and developmental biology. This conceptual expansion has been promoted in large part by theoretical, methodological, and empirical advances in two seemingly disparate fields. The first field is molecular biology, which opens powerful new windows on phylogenetic relationships, genome structure and function, and developmental mechanisms. The second field is paleontology, which affords a unique, direct, and expanding source of information into the anatomies, ecologies, physiologies, and spatial and temporal dynamics of past life. The fossil record is certainly rich in incident and rife with bizarre players, but an extensive body of research now treats the fossil record as a biological laboratory for rigorously framing and testing hypotheses at the intersection of paleontology with diverse disciplines across the full range of timescales encompassed by the earth and life sciences. This Special Feature collects some of the exciting and important new directions and insights, from the beginnings of life on Earth to the immediate precursor to the present-day biota (Fig. 1).

Paleontology informs the natural sciences by providing unique sources of data on important phenotypes and on the spatial and temporal dynamics of biological events and processes. Accordingly, we organize these contributions in terms of the important phenotypes contained in the fossil record, and the analysis of dynamics of species, clades, and communities in both space and time.

Phenotypes

At its most fundamental level, the fossil record is a narrative of changes to phenotypes and their functions: the origin, persistence, and demise of biological form (1–4), along with changes in behavior, physiology, and life history of vertebrates, invertebrates, plants, fungi, and protists (5–14). The contributions of paleontology to the study of the rates and pattern of phenotypic evolution are legion. At the species level, the fossil record has famously shown that the evolutionary responsiveness of local populations on decadal or centennial timescales usually translates at the 1- to 10-million-y timescale into stasis or nondirectional random walks rather than sustained, directional evolutionary transformation (15, 16). For higher taxa, the quantification of form within a multidimensional morphospace was developed in paleontology (17) and this rich literature continues to find new ways to explore evolutionary diversification, from formal visualizations of evolutionary convergence and parallelism (e.g., ref. 18) to direct analyses of the relation between ontogeny and phylogeny (19–21).

The biological world we see around us today is a highly pruned version of a rich and ancient tree of life. Consequently, reliance solely on recent taxa in analyses of origins can definitively mislead. The diversity and disparity of many extant clades, from elephants (22) to horses (23), and for that matter hominins (24), has demonstrably declined in the latest Cenozoic. Those clades were hardly unique, so that fossil data are essential for a fuller understanding of the rates and patterns of phenotypic change within and among many clades (e.g., refs. 25 and 26). Of course, some clades are inaccessible or sparsely represented as fossils, but even in such groups, from onychophorans to ants to penguins, fossils alter our picture of the timing and extent of morphological diversification. Formal incorporation of sparse fossil morphologies in phylogeny-based analyses of extant species is a promising interdisciplinary growth area (e.g., ref. 27).

Extinction can generate a false signal regarding the origin of evolutionary novelties when only extant taxa are analyzed (28, 29). For example, phylogenetic analysis of extant chordates suggests that bone evolved following the split between sharks and bony fishes, but the fossil record shows that bone was present well below that evolutionary node, and that modern sharks represent a derived state for the clade, having lost bony structures widely distributed in their ancestors (30, 31). Paleontological data are invaluable for inferring ancestral character states and the assembly of character complexes, and can now be used to test hypotheses drawn from developmental or phylogenetic analyses.

The discovery and analysis of fossils from key intervals in the history of life can inform the sequence, pattern, and phylogenetic dynamics underlying the origin of major functional and anatomical novelties. Such "intermediate forms" in the fossil record can serve as tests of genetic, developmental, and biomechanical hypotheses based on extant taxa. Indeed, some of the most fundamental discoveries of fossil stem taxa have only happened in recent decades. Among vertebrates alone, fossils have illuminated evolutionary pathways leading to the origin of vertebrates (32), tetrapods (33), turtles (34), snakes (35), mammals (36, 37), birds (38), horses (23), whales (39, 40), hominids (24), and many other groups. These fossils are valuable on several counts: (*i*) they provide data on the rate and pattern of character acquisition, which in turn illuminates the factors underlying dramatic transformations (e.g., feathers as insulation and display before flight in birds); (*ii*) they inform mechanistic hypotheses on underlying changes in development, both constraining and inspiring experimental tests of rival scenarios (e.g., developmental hypotheses on the origin of the wrist and ankle joints of tetrapods); and (*iii*) they place transitions in their environmental context (e.g., whales on the shoreline of a tropical sea (39) and hominids arising with bipedal gaits in woodland settings (41). Moreover, many major transitions occurred in ecosystems lacking close modern analogs, and so can be understood ecologically only by paleontological analysis of the peculiar ecosystems of their times.
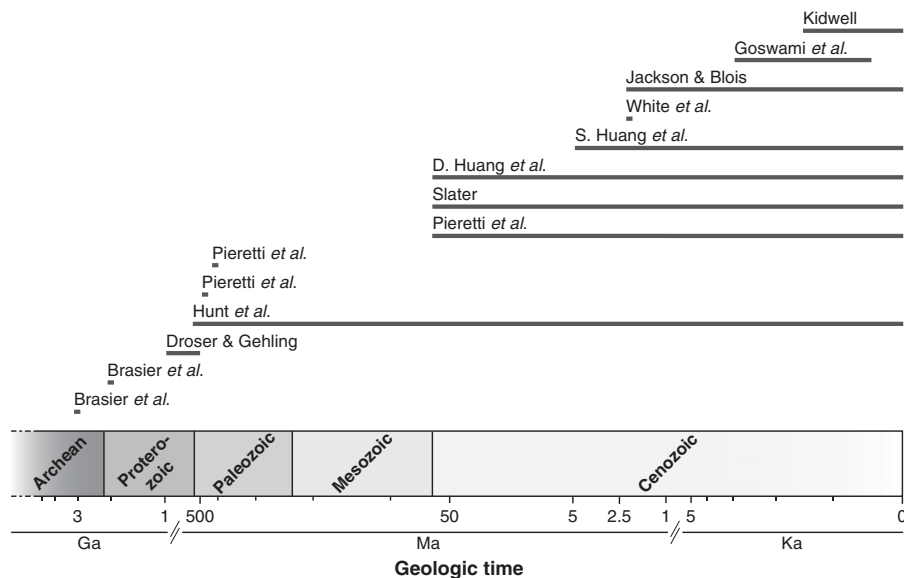
Fig. 1. Distribution through geologic time of the contributions to this Special Feature. Ga, billion (10^9) y ago; Ka = thousand (10^3) y ago; Ma, million (10^6) y ago.

Examples include the origin of vertebrates, arthropods, mollusks, and echinoderms (among others) in late Proterozoic and Cambrian seas with the initial establishment of macrofaunal foodwebs (42), the Paleozoic-early Mesozoic diversification of major insect clades in a world before flowering plants (43), and the protracted evolution of oceanic ecosystems lacking the mineralized phytoplankton that only became major factors in the late Mesozoic and Cenozoic (44).

Time

Rates and timing of taxonomic diversification within and among lineages can sometimes be inferred using data on extant organisms alone, and the vast comparative biology literature has detected many linkages between intrinsic biological traits and diversification rates in phylogenies of extant taxa (reviewed in refs. 45 and 46). However, decomposing diversification rate into its origination and extinction components is crucial for a wide range of issues, from niche conservatism to diversity-dependence (47–49). Such data are difficult to retrieve robustly from extant species because, for example, correlations between rates and individual or clade-level traits may undermine parameter estimates from phylogenies (50, 51), and extinction can mask true evolutionary rates or trends relative to those inferred from extant species (e.g., refs. 29 and 52–55). The fossil record can get closer to the mechanistic underpinnings of present-day biodiversity by providing direct observations on how and when clades differ in origination and extinction rates, and how both variables, and their relation to intrinsic

traits, can change over time (e.g., refs. 56–59). This paleontological access to long-term evolutionary dynamics allows empirical evaluation of multilevel evolutionary processes, and the relative contribution of traits at organismic, species, and even clade level in the waxing and waning of clades through time (2, 7, 60, 61). A major area of ongoing work on this general topic involves the integration of paleontological and molecular phylogenetic data, particularly when one or the other is sparse, and many new approaches and results are coming online (e.g., refs. 27 and 62–66).

Regarding extinction, the fossil record reveals that complex, seemingly robust ecological systems can collapse and take millions of years to recover. It also shows that when major extinction events occur on a global scale, recoveries are far more heterogeneous than expected: some surviving clades rediversify prolifically, whereas others linger at low diversities or slip into extinction long after the initial bottleneck (67, 68). Abrupt biotic transitions also occur at regional scales, and far more frequently than the attention focused on the Big Five mass extinctions of the geologic past might suggest. The fossil record associated with, for example, the late Cenozoic aridification of the North American interior (69), the uplift of the Himalayas (70), and the uplift of Panama (71) provides opportunities for comparative analyses of the biotic response to changing temperature, moisture, and productivity regimes, quantifying timescales and among-clade dynamics of diversity loss and recovery, and testing alternative drivers. The fossil record is as

much a document of clade failure as success, and provides a direct observational window on a wide range of natural experiments, in deep time and directly preceding the present biological moment.

At the same time, another key finding from the fossil record is a lack of extinction where it might be expected. For example, one of the great contributions of fossil data is the demonstration that species tend to respond to climate changes by individualistic range shifts, despite the web of positive and negative interactions seen in every present-day site. Thus, biotic associations have been disbanded and assembled during repeated glacial cycles without significant extinction or evident disruption of energy flow through novel ("non-analog") systems (72). The addition of anthropogenic pressures—not the least migration barriers in the form of highways, cultivated land, and cities and suburbs—has the potential to overturn such resiliency, and paleontological data on what biotas "want to do" in response to climatic and other drivers provide a valuable baseline perspective from which to view the likely acceleration of future species movements. Larger-scale biotic interchanges, which were often asymmetric between donor and recipient regions in the geologic past as they are today (73), further allow comparative evaluation of the major determinants and long-term consequences of successful range shifts of different magnitudes. At least one marine interchange through an ice-free Arctic Ocean has already occurred (74), and further analyses of that event in advance of its likely re-enactment in the near future (75) would be valuable.

The temporal perspective afforded by the fossil record has additional applications for predicting change and managing biodiversity. For example, biological baselines used to set conservation or restoration targets generally rely on the earliest sustained record-keeping in a target region, but this approach is severely limited relative to the trajectory of anthropogenic change at most locations. The nascent field of conservation paleobiology is demonstrating more profound shifts in natural systems from prior removal of key species and disruption of habitats and biogeochemical cycles by agriculture, fisheries, and industrialization (76, 77). In addition to community-level perspectives, close study of the environmental and biogeographic history of individual species is often feasible. For example, the European bison (*Bison bonasus*) has been managed as a forest specialist, but the fossil record suggests that its woodland distribution was only recently created by the loss of its open grassland habitat (78). As in

all of the topics touched upon here, the exchange of methods, data, and ideas should be a two-way street, and conservation paleobiology will benefit by the infusion of molecular methods and the continuing development of ecological and evolutionary models (48, 79).

Space

Clades are dynamic not only over time but through space. Although spatial variation in sampling can be as large a challenge in the fossil record as it is for many components of the modern biota (80), the fossil record of even sparsely preserved clades can significantly inform the biogeographic and environmental history of lineages and major groups. The geologically recent presence of horses, proboscidians, and rhinos in the New World (81) and, in the early Cenozoic, monotremes in Argentina (82), ratites in the Northern Hemisphere (83), hummingbirds in the Old World (83), mousebirds in North America (84), *Acropora* reef corals in Britain (85), and the huge (up to 1 m) campaniloid snails of southwest Australia in California, the Caribbean, Africa, and northwest Europe (86), are just a sampling that demonstrates the pervasive history of biotic expansion and regional extinction that would be difficult or impossible to infer from present-day diversity and distributions. The paleontological data can now feed into new models for the spatial and temporal dynamics in their respective clades, and the history of biodiversity hotspots and coldspots can become much clearer (87–90). These data also suggest that macroecological and macroevolutionary analyses of present-day regional biotas may be better informed by incorporating geologically recent extinction and origination into the equation rather than under an equilibrium assumption a priori (48, 91–93).

Just as the fossil record has provided rich evidence for the highly clumped distribution of originations and extinctions through geologic time (e.g., refs. 42 and 47), spatially explicit paleontological data have shown that evolutionary novelties and major clades preferentially originate at low latitudes (94, 95), and perhaps certain environments in both marine and terrestrial settings (95–97). Large-scale diversity trends along latitudinal and other environmental gradients are thus shaped not just by in situ origination and extinction but also by the export of lineages into novel habitats, in violation of the general tendency toward evolutionary niche conservatism seen in most clades. This is an especially active area for interdisciplinary work: spatially explicit phylogenetic analyses incorporating fossil and extant taxa (98) will go

far in elucidating the mechanism and significance of these patterns.

Analyses that combine phenotypes with temporal dynamics in a spatially explicit context are rare but are likely to increase with new methods and datasets. In a pathfinding study, Hellberg et al. (99) showed that present-day populations of a marine snail diverged significantly in form from its late Pleistocene predecessors, generating a variety of novel shell forms with postglacial range expansion. This exemplary study combined phylogeographic analysis with comparative morphometric analyses within a single species before and after range expansion. Only by coupling analyses of phenotypic diversification in both space and time will we be in a position to achieve a mechanistic understanding of ecological and evolutionary changes across scales, from local to global, and hierarchical levels, from molecules through bodies to species and clades (2).

Introduction to the Papers in This Special Feature

The papers assembled in this Special Feature, which range in time from the earliest vestiges of life in Archean sediments to the fossil record accumulating from extant species communities (Fig. 1), can be roughly organized as mainly concerned with origins or dynamics.

Origins. Brasier et al. (100) discuss the technical and conceptual advances in the search for the earliest fossil traces of life. Microfossils have long been reported from the Archean Eon [3.5–2.5 Ga (= billion y)], but new techniques for imaging and nanoscale elemental analysis, growing knowledge of present-day prokaryote phylogeny and diversity, and close attention to the environments and processes of microorganism preservation are pushing this field forward. Brasier et al. discuss refined criteria for separating preservational artifacts from fossilized prokaryotes, and revisit three classic microbiotas. The authors reject the biogenicity of many specimens from the Apex Chert (a controversial assemblage dated at 3.46 Ga), and document a microbiota from the roughly contemporary Strelly Pool Sandstone (dated 3.43 Ga), unexpectedly preserved between sand grains from the earliest known shoreline. These shore deposits seem unlikely hosts for cellular preservation, and so these finds open a new search window for the early fossil record and expand our ecological picture of early microbial life. High-resolution imaging in one of the classic younger microbiotas, the Gunflint Chert (1.88 Ga), confirms that the

problematic microfossil *Eosphaera* represents a form unknown in modern biotas, likely an extinct experiment in microbial multicellularity.

Droser and Gehling (101) synthesize data on the Precambrian assemblage of multicellular fossils known as the Ediacarian Biota. With a near-global distribution from >40 localities in rocks 575–541 My, these fossils offer a picture of early multicellular life about 30 My before the famous Cambrian Explosion. An enigmatic array of forms, the Ediacarian Biota have spawned numerous controversial hypotheses about their relationship to extant clades, and their significance for understanding the rise of multicellular life in general. Droser and Gehling show that the Ediacaran forms, whatever their phylogenetic affinities, present many attributes of later animal life, including mobility, heterotrophy, skeletonization, and participation in complex ecosystems, and so these forms offer an informative comparator to later animal evolution. Moreover, because the biota includes, in addition to many phylogenetically problematic taxa, early relatives of cnidarians, poriferans, and bilaterians, it sheds light on the roots of the metazoan radiations of the Cambrian and later times.

Pieretti et al. (102) demonstrate the power of combining the growing morphological and phylogenetic records from the fossil record with novel technologies in development and genomics to provide a richer understanding of major evolutionary transitions. With continued discovery of new fossils and fresh perspectives on others, and the expansion of developmental and genomic analyses beyond standard model organisms, this multidisciplinary approach can be applied to many of the long-standing questions of anatomical evolution. Focusing on the evolution of vertebrate appendages, Pieretti et al. first present evidence that the origin of paired, lateral appendages in vertebrates involved a redeployment of the developmental program for a single median fin, initially generating a paired set of pectoral fins and only later giving rise to the pelvic appendages. The transition from fins to limbs is well-documented in the fossil record, and we can see that the defining feature of limbs, the wrist, and digits, arose in a series of evolutionary steps in an extinct lineage of sarcopterygian fishes. The wrist and digits have no clear morphological counterparts in extant fishes, and the underlying developmental and genetic transitions are obscured in model species of teleost fishes because of genome duplication and reorganization in that clade. Experiments using gar (which separated from the teleosts before the duplication event)

show that its regulatory enhancers can drive digit development in mice, suggesting that the wrist–digit complex and its regulatory pathways did indeed have homologs in the distal bones of early bony fishes. Changes in gene regulation can also be traced through diversification of limb design, and analysis of mammalian digit reduction, a common evolutionary theme, shows that convergence on reduced digit number has occurred by two very different genetic and developmental mechanisms, giving insight into the remarkable malleability of vertebrate limbs. The next step in the integration of paleontology and developmental biology may well be the experimental modulation of gene expression to test specific hypotheses on transitional forms and their underlying genetic basis against fossil phenotypes close to those transitions.

White et al. (41) show that a priori assumptions about what evolutionary ancestors should look like can be misleading in our understanding of human evolution. Biologists have long assumed that the immediate ancestors of the human clade were chimpanzee-like. The discovery of *Ardipithecus* challenges these assumptions on multiple levels. By revealing both unexpected morphological conditions and ecological provenance, this discovery reveals an informative complexity to hypotheses of morphological transformation and adaptation during the acquisition of traits unique to humans.

Dynamics. The empirical analysis of evolutionary tempo and mode has been one of the great contributions of paleontology. Phenotypic stasis has proven to be far more prevalent than expected, and the challenge is now to rigorously test alternative evolutionary models for long-term phenotypic evolution and seek explanatory mechanisms for the different trajectories exhibited in fossil time-series. Hunt et al. (103) fit likelihood models to a large compilation of evolutionary studies ranging in scope from 5,000 y to >50 My. The authors again find that stasis and random walks best account for temporal patterns, rather than directional change, but also show that more complex models—particularly stasis plus punctuational change, and shifts from a random walk to stasis—tend to be increasingly supported in a maximum-likelihood framework with increasing numbers of samples within a study. Stasis is more prevalent in marine than in terrestrial settings, and in macroinvertebrates and vertebrates than in microfossils. Evaluating the role of external drivers, Hunt et al. simulate phenotypic sequences using a model in which traits track an empirical long-term climate curve. The frequencies of

evolutionary modes in the simulated sequences are quite similar to those in the real data, suggesting that the bounded, often oscillatory, nature of many physical environmental changes contributes significantly to the nondirectional dynamic observed in many fossil sequences.

Goswami et al. (104) explore the ways that morphological characters are integrated developmentally into a unified, functioning organism, and how this integration influences and is influenced by evolution. The authors argue for the importance of a deep-time perspective to the analysis of integration, modularity, and the origins of morphological variation. Taking advantage of the large mammal populations preserved in Late Pleistocene tar pits, Goswami et al. analyze the evolutionary signal of patterns of phenotypic integration in dire wolves and saber-toothed cats from different pits spanning 27,000 y of evolution at Rancho La Brea. These samples reveal decreasing levels of phenotypic integration as climate changed, indicating that developmental interactions created—or failed to damp—increasing phenotypic variation in responses to stresses associated with environmental change.

A long-standing issue in biodiversity dynamics is the potential operation of negative feedbacks: Is the rate and level of taxonomic or phenotypic diversification itself diversity-dependent? This question is difficult to resolve definitively using comparative phylogenetic data on extant taxa because extinct species cannot enter into diversity or disparity estimates through time. Slater (105) tests for diversity-dependent morphological diversification in the dog family, Canidae, a group with an excellent fossil record that exhibits three sequential diversifications through their 40-My history in North America. Diversification slowdowns are generally viewed in terms of declining ecological opportunities as the "ecological barrel" gets filled, and fossil canids can be studied in terms of dietary diversity based on dentition and body size. Slater finds support for neither an early burst of evolution and subsequent diversity-dependent slowdown, nor for unconstrained diversification fitting a Brownian motion model. Instead, the North American canids best fit a multipeak Ornstein–Uhlenbeck model, where clades gravitate toward specific trait values, in this case three different body-mass and tooth-area values, one for each of the major dietary categories within the Canidae. These results can thus be interpreted as a set of replicated diversifications, occurring in and among three stable, bounded adaptive zones. Thus, apparent

early bursts in phenotypic evolution could derive not only from an evolutionary slowdown in an increasingly crowded world, but from constant evolutionary rate within a bounded morphospace. Those bounds might be set by intrinsic, developmental constraints, the presence of phylogenetically unrelated but ecologically similar competitors, or by climatic and other environmental changes that continually shift the ecological space that can accommodate different dietary groups over time. Diversity ceilings may exist but are moving targets on macroevolutionary timescales, as others have suggested in various contexts (e.g., refs. 47, 106, and 107).

Regional biotas are shaped by the interaction of origination, extinction, and immigration, so that present-day diversity and its relation to current environmental factors can only tell part of the story. S. Huang et al. (108) use the rich Pliocene record (2–5 My ago) on the warm, temperate coasts of North America to evaluate the dynamics leading up to the modern distribution of marine biodiversity. With marine bivalves as a model system, the authors show that overall regional diversities were shaped by extinction and subsequent recovery through origination and immigration, with clades (here, taxonomic families) shared by the two coastlines showing a variety of divergent, convergent, and parallel trajectories in species richness. Thus, similar diversities for a given clade in different regions today is no guarantee of a shared history or similar diversification rates, and differences might be geologically recent rather than stemming from deep-seated evolutionary differences. S. Huang et al. find that the contribution of regional extinction to today's species-richness patterns can be predicted by the geographic range sizes of species during the Pliocene, a variable difficult to extract from present-day data but likely to play a role in extinction risk with the onset of large-amplitude glacial cycles near the Plio-Pleistocene transition. Past distributional shifts (i.e., local or regional extinction and immigration) are crucial to interpreting present-day biogeography.

Extinction does more than remove phenotypes and their ecological roles: it erases evolutionary history (EH). This effect is of interest in its own right; for example, the marine extinctions that accompanied mid-Cenozoic polar cooling were more evenly distributed phylogenetically in the Arctic than in the Antarctic, so that similar regional extinction intensities removed significantly more EH in the Southern Ocean than in the Arctic (89). However, EH can also be a basis for conservation decisions, with regions or clades prioritized in part by the amount of

EH they represent. D. Huang et al. (109) address for the first time one of the major conceptual and methodological gaps between molecular and phylogenetic approaches to origination and extinction, and assess how these contrasting approaches affect estimates of EH and its loss. Molecular phylogenies, which depict the splits created by differentiation of gene pools in extant species, necessarily yield bifurcations. Paleontological phylogenies, which reflect the phenotypic stasis and nondirectional change that pervades the fossil record, often incorporate a budding evolutionary topology, with lineages persisting after new species have split from ancestral populations or clades. Using simulations, D. Huang et al. find that estimated losses of EH in major extinction events are qualitatively similar when extinctions are random with respect to clade age, although EH is lost more rapidly with increasing extinction intensity in paleontological data than in molecular trees. When extinction focuses on older lineages, as appears to be happening today, both approaches capture the disproportionate erosion of EH, although the molecular signal is damped relative to the paleontological one. Using a phylogeny of living and extinct scallops from California, which have an exceptional fossil record, the authors find a preferential loss of young species in the Plio-Pleistocene extinction pulse, although this signal proves difficult to retrieve from molecular data, consistent with simulation results. Nonetheless, the encouraging outcome of this study is that extinction selectivity measured by these different approaches to EH are broadly comparable, indicating that the fossil record can provide a useful natural laboratory for anticipating future losses of EH caused by anthropogenic extinctions.

At a finer scale, ecological communities are also shaped by origination, local extinction, and immigration. Jackson and Blois (110) consider how these factors shape terrestrial community composition and how an understanding of the incessant change in communities documented in the Quaternary fossil record—the past 2.6 My—can inform both ecological theory and the management and conservation of terrestrial biodiversity. Climate changes can be gradual and directional, but are often punctuated by episodic events and by rapid-state transitions, and detailed pollen records show that some communities accordingly disassemble gradually via decline and replacement of dominant species, whereas others undergo rapid collapse and turnover. Similar data for insects and vertebrates reinforce this perspective, that local biological communities are "passing

manifestations of ecological and biogeographic processes in a world of ceaseless environmental change" (110). Rates of change have varied greatly over time and among communities through time the past 20,000 y, and the implications of these strong variations are only beginning to be explored and appreciated. While highlighting the abundant paleoecological support for environmental drivers for community composition, Jackson and Blois emphasize that even the broadest spatial patterns are spatial aggregations of local interactions among populations of competitors, predators, mutualists, and parasites. Such interactions govern community outcomes of environmental change, and more work is needed that takes into account interactions—and the traits that mediate them—in relation to environmental drivers. Still unclear, for example, is whether communities can display stability in the functional attributes of their components even as species composition ebbs and flows. Integrated study of paleoecological case studies would test fundamental ecological theory and provide insights for how and where anthropogenically driven activities might be overriding past controls on community dynamics.

In our final paper, Kidwell (111) examines the many ways in which very young fossil records from the last few decades to millennia can provide unique insights into the current status of extant species, communities, and biomes, emphasizing marine and coastal systems. The fossil record of the Anthropocene—the informal term encompassing the human domination of a majority of natural processes on a global scale—includes information from still-unburied organic remains as well as shallow-cores, thus linking directly to older fossil records. Such approaches provide baseline ecological data otherwise inaccessible by direct observations and written records, and permit the roles of natural and anthropogenic drivers to be assessed in situations both outside and within the timeframe of diverse human impacts. Kidwell notes that virtually all biological systems, even in the most remote areas, today operate around anthropogenically driven environmental trends rather than stationary

means, and argues that the interaction of climatic with other human stressors, rather than climate change alone, is creating the apparently unique dynamics in today's biota. Analyses of shifts in abundance, diversity, and ecosystem function in fossil records document unprecedented biological change within the last few centuries relative to the past 2 My, linked to human expansion and technological advances. Kidwell calls for an integration of paleontological data on the dynamics of extant species, communities, and ecosystems on recent decadal to millennial timescales, which had once been viewed as outside the paleontologist's purview, with ecological theory and management of the biological world.

The Future of the Fossil Record

The future of the fossil record is as many-faceted as the disciplines that it impacts. A wide range of research questions involving biological systems can benefit greatly by incorporating data from the fossil record. Many exciting directions could not be included in this Special Feature, from ancient DNA (112, 113) to biomechanics (114–116), to positive and negative feedbacks among clades (117–119) and between biological systems and the global environment (5, 42, 120). By bringing together papers at the forefront of the integration of paleontology with other disciplines, we hope this Special Feature will help define a future agenda for work at these scientific interfaces.

Sadly, as this volume went to press we learned of the tragic death of one of our contributors, Martin Brasier. Martin was an integrative paleobiologist *par excellence*, who made fundamental contributions to many aspects of paleontology, most recently regarding the early evolution of life, from the interpretation of the oldest fossil evidence of living things to the biology of the enigmatic Ediacaran Biota. He will be missed.

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