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Biodiversity

A call to the custodians of deep time

Palaeontologists must model the causes of biodiversity rather than simply cataloguing fossils, says **Douglas Erwin**, as they curate the only record of ecosystems undamaged by humans.

Humans have been destroying much of Earth's life for the past 10,000 years. It might be comforting to think that we have a reasonable grasp of the factors lying behind the planet's number of species and their abundance, should we ever choose to reverse this course. But to a large extent, we don't.

Today, ecologists can look at the biodiversity of tropical forests and compare that with polar regions, listing the reasons for the differences they find. But in the fossil record the picture of diversity is more confused. Palaeontologists cannot even agree whether diversity was higher 10,000 years ago than it has ever been, or whether it plateaued hundreds of millions of years ago. The confusion persists because palaeontologists continue to simply look for patterns in the fossil record, which is incomplete and subject to interpretation. Instead, we should be seeking to study the basic processes that underlie diversity, and building models to test those theories. Only by understanding what governs diversity can we settle old arguments about how it has changed over time.

The debate over which scenario is correct has an impact on fundamental questions about how evolution builds biodiversity and the importance of evolutionary innovations. Has the ecological space occupied by Earth's biota expanded over time, or has it simply become more crowded? Does intra-species competition keep diversity in check, or does the creation of one species construct new environments and opportunities for others, allowing diversity to bloom?

Today, palaeontologists are the custodians of the only record of ecosystems undamaged by human activities. In 2006, palaeoecologists found that modern, human-modified Caribbean reef ecosystems are completely unlike any reef community of the past 220,000 years[1]: studying modern Caribbean reef ecosystems leaves us blind to how they originally operated. The same is true, I am sure, of other ecosystems. Although the fossil record is far from perfect, it is perhaps the best resource for understanding the processes involved in the development of biodiversity, and the only record that we can use to evaluate the long-term significance of competition and evolutionary innovation. To do so, those interested in the history of life must move beyond collecting fossils to creating models.

Life on Earth is some 3.5 billion years old. Before oxygen levels rose in the ocean and atmosphere some 600 million years ago, global diversity was probably limited. The macro-fossil record begins in earnest with an explosion of animal life some 575 million years ago — just before the start of what is called the Phanerozoic eon around 540 million years ago. This culminated in the 'Cambrian explosion' (535–520 million years ago). Since then there have been several periods of apparent rapid increases in diversity, as well as stunning mass extinctions that eliminated many evolutionary lineages. All of the non-avian dinosaurs, for example, were killed at the end of the Cretaceous period 65 million years ago.

The fossil record is dramatically incomplete, at all scales. In the metaphor of Charles Lyell and Charles Darwin, it is as if we have only a few chapters of a book, and but a few pages of each chapter with only some fragmentary sentences on each page. I would say the record is a bit better than that, but it remains true that in any one place there is more time missing than there is preserved.

> "Only by understanding what governs diversity can we settle arguments about how it has changed."

The vagaries of the fossil record have led to differences in interpretation. Since Oxford palaeontologist John Phillips first chronicled the fossil record in 1860 (see graphic, below), most have assumed that diversity has grown over time, particularly over the past 100 million years. But in 1972, palaeontologist David Raup of the University of Chicago argued that marine diversity might well have reached a plateau over 400 million years ago; the apparent increase since then, he argued, was an illusion created by increasingly better preservation of fossils in younger rocks.

A 1981 paper in *Nature* by Raup and many of the other protagonists in this debate led to an uneasy consensus in favour of strong increases in diversity in the early Palaeozoic (542–252 million years ago), and again over the past 100 million years[2]. For several decades Raup's concern bubbled away in the background as palaeontologists compiled steadily more detailed databases of the durations of fossil families and genera, based on the oldest and youngest known samples of each. The most comprehensive of these was constructed by the late Jack Sepkoski, also of the University of Chicago, and includes more than 37,000 genera.

Sepkoski concluded that there was a roughly linear, several-fold increase in diversity through the Phanerozoic, which he believed would ultimately level out[3]. Others analysing the same data argued that global diversity had expanded exponentially, particularly over the past 100 million years or so. In July 2008, results from the Paleobiology Database project (http://paleodb.org), which aims to collect a record of all fossil finds, built up location by location, and includes 3.5 million records, suggested that recent marine biodiversity is only 1.5–1.8 times the average of the Palaeozoic[4] — much less than some expectations.

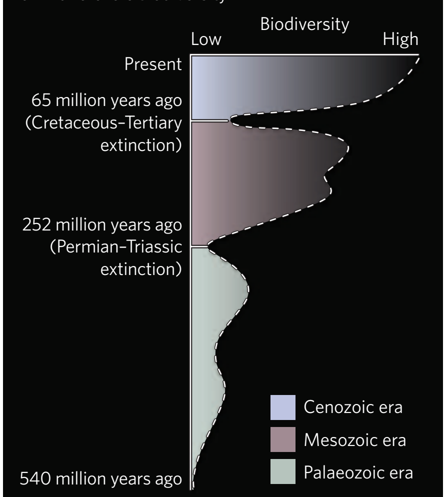
In the absence of any expectations about what sort of diversity pattern we should expect to find, it is difficult, if not impossible, to tell which reconstruction of Phanaerozoic diversity is correct.

Ecological spaces

Palaeontologists often say that a burst of diversity in the fossil record simply 'filled in ecological space', as if each new species simply took up residence in a square of a pre-existing chessboard. This would match Darwin's notions of intra-species competition being the main driver behind how life fits into ecological niches, and would imply that diversity should grow only slightly over time.

AN 1860 RECONSTRUCTION OF THE FOSSIL RECORD

The first of many, hotly-debated, estimates of Phanerozoic biodiversity.



J. PHILLIPS LIFE ON THE EARTH: ITS ORIGIN AND SUCCESSION (MACMILLAN, 1860)

I think a much better analogy is of building the chessboard itself. Although some of these ecological spaces may exist independently of any species that occupies them, many more are defined by species and their mutual interactions. I would argue that the chessboard grew during the Cambrian diversification, for example, increasing its overall ability to support life. Thus we should expect significant increases in biodiversity over time, particularly when adaptive breakthroughs open up new opportunities or construct new habitats such as reefs.

How does such a chessboard grow? As a first step in answering this question, first-order, process models of global biodiversity need to be developed that are informed by our understanding of past climates, continental configurations, and geochemical cycles. For example, diversity is much higher near the equator than near the poles. So we might predict there would also have been greater diversity at times in the past when the area of tropical marine shelves was greater, or during global warm periods. However, warm periods might also lead to nutrient-trapping in continental basins and the spread of oxygen-free waters, thus restricting diversity. The number and position of continents, each carrying its own ark of species, is another important variable. Basic models should be built in which the input of such variables can reliably predict biodiversity at various places and times.

What spurred brachiopods to such diversity?

SMITHSONIAN INSTITUTION/D. ERWIN

Additions will then be needed to address ecological interactions. Ecologists have begun work on models of diversity, some of which have spurred an ongoing debate about the importance of niches in biodiversity. Ecologists have also examined how organisms such as corals construct habitats for other organisms, thus boosting diversity. But ecologists have only begun understanding these processes over the past decade, and palaeontologists have done very little to explore their application to deep time. My colleagues and I, for example, are studying the role of ecosystem engineering in the Ediacaran–Cambrian diversification of early animals (579–510 million years ago). My suspicion is that some evolutionary innovations have disproportionate effects on diversity — the advent of burrowing behaviours, for example, might have changed marine sediment chemistry and microbial productivity in ways that spurred further innovation. But for now we have only qualitative arguments.

Models built to examine these ideas will need to be tested empirically, so we need to ensure that data are being collected in an appropriate way for future use. If, for example, a model is built to look at the effects of filtering sponges and clams on water quality and subsequent diversity, then simply knowing that those animals lived at a given place and time will be insufficient: the number of sponges and clams will also need to be determined. But this information isn't always captured. One of the world's largest palaeobiology collections, for example, contains more than a million fossils gathered by G. Arthur Cooper and Richard E. Grant in west Texas from the 1930s to the 1980s, but doesn't contain sufficient information to determine the relative numbers of fossils in the various stratigraphic layers. This is a huge loss to the field. Today, palaeontologists are more likely to count the numbers of fossils they find in each rock layer and use the same approach from one location to another. But this is time-consuming, and not always done. This needs to become standard.

Any understanding of dynamics also requires a firm knowledge of when things happened in the fossil record, and for how long. Very-high-resolution radiometric dating (accurate and precise to 0.1% or better) is an appropriate tool (see EARTH-TIME.org).

Model culture

Such model building would come naturally to physicists. When they designed and built an instrument to look for the Higgs Boson, for example, they did not plan to simply turn it on and sift through all the data; they developed models to help them predict what they might see if certain theories about the Higgs were true, and they will match their collected data to their predictions. Palaeontologists do not tend to think like this.

Palaeontologists share a common interest in the dynamics of growth with economists. Although the global recession has dealt a blow to economic modelling, basic lessons can still be learned from the beginnings of the field. Early models of economic growth were incredibly simple, focusing on the numbers of workers, for example, without any consideration of how those workers might interact. When combined with empirical data, the models provided great insights into economic growth (and won their developer a Nobel prize). In these early models, sustained economic growth was achieved only by adding an arbitrary variable for technological innovation; economists eventually unpacked the processes of economic growth by opening this 'black box' of technological innovation and deconstructing the processes that drive it. The lesson to learn is that relatively simple equations, if properly constructed, may explain much of an observed pattern, allowing researchers to focus on the unexplained portion.

Palaeontologists need to adopt a similar approach. Building simple, 'toy' models of biodiversity will be relatively easy. Developing more sophisticated approaches will be a job not just for palaeontologists, it will also require the input of geologists and, more importantly, physicists and theoretical biologists.

My palaeontological colleagues may object that diversity is far too complicated, but that is of course the point of good process-oriented models, for they extract from complexity the critical variables that are believed to control the dynamics. Through iteration with empirical testing the models will improve, and provide an important spur to future research.

To get the full picture of biodiversity, we must explore the fossil record. But we must do so deeply — burrowing beneath patterns in search of the processes that control diversity, and building models to test these ideas. ■

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See Editorial, page 251, biodiversity special at www.nature.com/darwin and palaeontology podcast at go.nature.com/UuNpgJ