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Macroevolution of ecosystem engineering, niche construction and diversity

Douglas H. Erwin[1,2]

[1] Department of Paleobiology, MRC-121, National Museum of Natural History, Washington DC 20013-7012, USA
[2] Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, NM 87501, USA

Organisms influence their environments through activities that range from bioturbation to modification of redox gradients and construction of structures. Some of these activities modify the selective regime of the builder (niche construction) and some influence the ecological success of other species (ecosystem engineering) as well as their evolutionary prospects. In this article, I argue that these processes produce effects that persist over geological time, modulating macroevolutionary patterns and diversity. Examples include greater sediment bioturbation and increased thickness and persistence of shell beds. The impact of these processes has been increasing over time, with recent communities encompassing greater ecosystem engineering than those of the early Phanaerozoic. Thus, positive feedback through environmentally mediated selection seems to have increasingly enhanced biodiversity through the Phanaerozoic.

Engineering diversity

That organisms actively modify their environments and influence those of other species is not a particularly novel observation. Organisms have been modifying their environments since the first microbial consortia over 3 billion years ago began trapping and binding sediment, altering their physical and geochemical environment and producing stromatolites and, eventually, the first reefs. But what is the long-term evolutionary impact of such activities and, in particular, have they had a crucial role in the construction of diversity?

Controversy has recently arisen over the ecological and evolutionary effects of such activity, in particular, regarding whether such activities have been adequately incorporated within standard evolutionary theory. Under the rubric of niche construction (see Glossary), some researchers have advanced the hypothesis that many activities of species produce persistent ecological modifications, or alter their own fitness and thus modify their evolutionary trajectories, through ecological inheritance [1–4]. Many activities also modify the physical environments of other species in a process termed physical ecosystem engineering, creating or destroying niches, altering resources and, thereby, altering the selective regimes of these taxa [5–8] (see Box 1 for a comparison of these concepts). These proposals have engendered considerable discussion but relatively little focus on their potential longer-term, macroevolutionary aspects.

Here, I begin by discussing the macroevolutionary dimensions of ecosystem engineering (which has previously been considered mostly from an ecological perspective) and argue that ecosystem engineering has increased over time, having an important role in increasing diversity. Niche construction has almost certainly increased as well but, given the difficulties in recognizing selective pressures in the fossil record, this is more challenging to establish. Consequently, I largely focus on the effects of ecosystem engineering and ecological inheritance (broadly defined), and take up the issue of identifying the changes in fitness associated with niche construction. Finally, I discuss evolutionary innovations involving ecosystem-engineering effects that have broad ‘spillover effects’ and propose that these are likely to have had a particularly important role in increasing diversity. Here, I am not concerned with whether macroevolution is distinct from microevolution [9] but with long-term trends and patterns in ecosystem engineering and niche construction. These activities have altered resource distributions and enhanced biodiversity through positive feedback. Although both marine and terrestrial examples are included, macroevolutionary patterns have been more intensively studied in marine ecosystems and hence these form the bulk of the examples.

Macroevolutionary ecosystem engineering

Physical changes in the environment are often mediated by biological activity and can directly influence the nature and composition of communities, both through direct

Glossary

Ecological inheritance: the persistence of environmental modifications by a species over multiple generations to influence the evolution of that or other species.
Ecosystem engineering: modifications to the environment by a species that affects resource availability for another species.
Facilitation: positive interactions between species to increase the persistence or abundance of either or both species.
Macroevolution: evolutionary patterns and processes above the species level.
Niche changing: organisms affect their environment and those of other species as by-products of their activities.
Niche construction: informed activities of organisms that influence the environment and affect the fitness of the population.

Corresponding author: Erwin, D.H. (Erwind@si.edu).

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Box 1. Niche construction versus ecosystem engineering

The concepts of niche construction and ecosystem engineering pose a challenge to Gould's adage that 'the organism proposes and the environment disposes'. To the extent that organisms alter the environment to their own benefit, this feedback eliminates any clear distinction between organism and environment, as initially recognized by Dawkins [42] and Lewontin [43].

Ecosystem engineering focuses on the ecological dimension, involving the modification of resource availability to other species by the activity of organisms that create, alter or destroy habitats [5,6]. Almost all species engage in some degree of ecosystem engineering, from the formation of shell beds by molluscs to the alteration of soil by worms.

Niche construction involves interactions between a species and its environment that modify the niche of the species and, thus, the selective pressures on the species. These modifications involve either moving to a more appropriate environment or physically modifying their selective environment. If such modifications persist to influence the selection of subsequent generations, they constitute ecological inheritance. Thus, compared with ecosystem engineering, niche construction is focused more on the evolutionary implications of the impact of species on their environment. Ecological facilitation theory also focuses on positive feedback between species but initially [44] neglected ecological inheritance and other evolutionary effects. Subsequent work has addressed some of these issues (reviewed in Refs [45–46]), but its macroevolutionary importance has not been explored.

Odling-Smee and colleagues view ecosystem engineering as a consequence of niche construction [3], but it is not clear whether engineering activities of organisms always have a selective impact on the species that induce them. Odling-Smee recognizes, however, that niche construction activities can benefit populations of the same species other than the one that engaged in niche construction or that the effects might be too remote in time to effect the original population (F.J. Odling-Smee, personal communication). In such cases, it is at least operationally useful to distinguish between the two categories. Dawkins [47] criticized niche-construction arguments for failing to distinguish between limited cases of true niche construction, where variation in niche construction are replicated with fidelity across generations and more common cases where organisms effect their environment and those of other species as by-products of their activities, which he describes as 'niche changing'. Turner has suggested a more complex interplay in which ecological inheritance – which he terms a 'persistor', in analogy to Dawkin's replicator – might influence the course of evolution when the persistence of the ecological inheritance is long relative to the duration of a replicator [48].

When niche construction involves active modification of the selective environment of a species it encompasses ecosystem engineering, but the presence of ecosystem engineering does not, it seems to me, necessarily involve niche construction. In assessing the macroevolutionary consequences of feedback between organisms and the environment, it seems useful to maintain the distinction between these two concepts. This distinction seems particularly important during biological innovations and major evolutionary transitions.

interactions and through feedback that persists longer than the ecological engineer [10]. In an ecological context, this is described as succession or facilitation but the phenomenon also has a longer-term, macroevolutionary dimension. The most significant ecosystem engineering processes from a macroevolutionary perspective are those that produce long-term, persistent environmental changes, or ecological inheritance, and some examples are described here.

Shell beds

The accumulation of shells and other skeletal debris on the sea floor is an example of taphonomic feedback [11]. Taphonomic feedback includes the facilitation of larval settling and adult growth by the provision of hard substrates for attachment and substrate stabilization for taxa requiring firm substrates. Comparison of the density of shell accumulations from the Ordovician–Silurian [489–416 million years ago (Ma)], Jurassic (199–145 Ma) and Neogene (23 Ma–present) has established a significant increase in the number and thickness of shell beds in marine siliciclastic environments through the Phanaerozoic (542 Ma–present) (Figure 1). This increase in shell-bed density seems to reflect the shift from brachiopod-dominated Ordovician–Silurian communities to molluscan-dominated Neogene systems [12]. Moreover, the shell beds are persistent. For example, studies of bivalves in the Colorado Delta of the Gulf of California shows that average duration of a dead shell on the sea floor is 661 years before it is either deeply buried or destroyed [13]. This transition increased diversity by the Neogene by enabling the accumulation of more species adapted to dwelling in shell gravel. Thus, the persistence of molluscan-dominated shell beds altered both the marine substrate and the composition of benthic communities, and did so in a way that persisted over very long time scales.

Burrowing and bulldozing

Burrowing organisms have both positive and negative effects on other species. Bioturbation increases the complexity of geochemical gradients in sediments through greater oxygen supply and shift in redox gradients. This, in turn, can greatly increase microbial biomass, attracting further bioturbators and expanding the zone available for bioturbation. The net result is more usable organic matter in the sediments [14], which can have a strong positive-feedback effect on biodiversity [15,16]. Organisms also employ turbulence and induced flow to accomplish physiological functions, leading Turner [17] to describe the architectural features as agents of 'extended physiology'. For example, the internal structures of both sponges and termite mounds and often their orientation on the landscape are constructed to maximize flow.

Although some simple surface trails made by animals have been discovered in the Late Proterozoic, active bioturbation began near the base of the Cambrian (542–490 Ma), during the explosive diversification of animal life [18] (Figure 2). A similar pattern has been documented on land, with limited bioturbation through much of the Palaeozoic, then a rapid increase in the range of environments and the architectural complexity of burrowing in the Carboniferous (359–299 Ma) [19]; curiously, freshwater habitats experienced little bioturbation until the post-Palaeozoic (younger then 252 Ma) [20]. Thus, in both marine and terrestrial ecosystems, there has been an increase in the extent of remodeling the sediment. Today, non-bioturbated sediments are usually restricted to anoxic marine basins and lakes, where burrowing organisms are excluded.

Increased burrowing through sediment can also be a negative taphonomic feedback. In his 'bulldozing' hypothesis, Thayer [21] documented the increase in burrowing through the Phanaerozoic and its consequences for immobile organisms living on unconsolidated sediment.

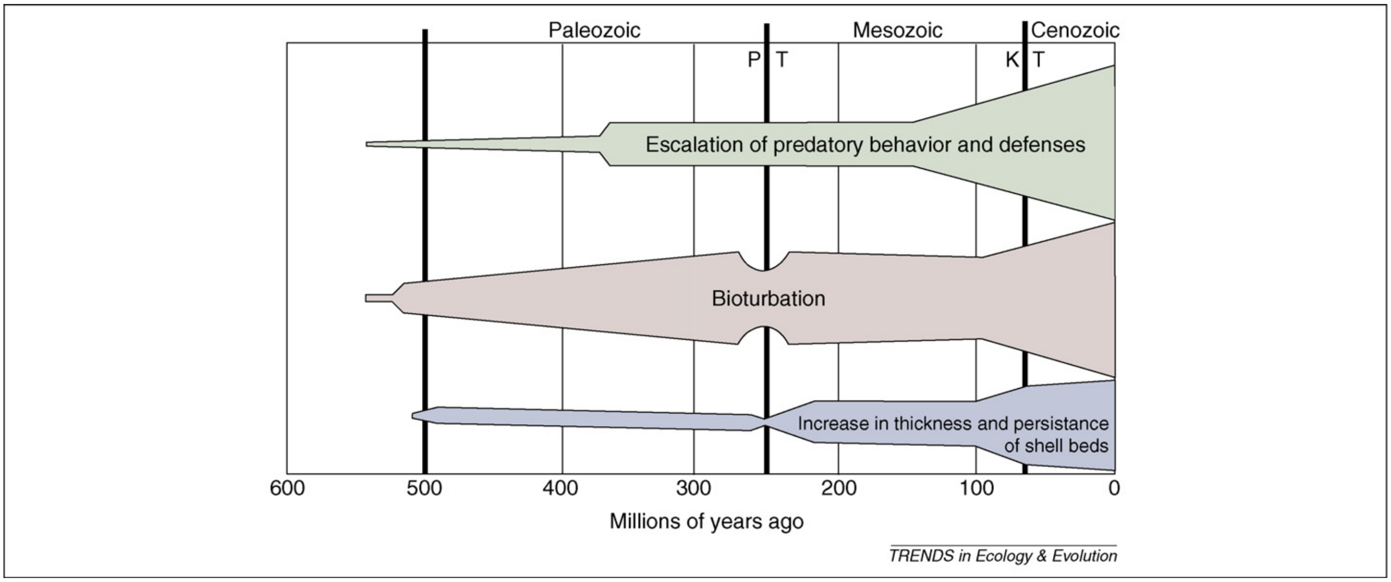

Figure 1. The extent of ecosystem engineering and niche construction has changed through the Phanaerozoic, and evidence indicates that, at least within marine ecosystems, ecosystem engineering has increased since the Cretaceous. The escalation of interactions between predator and prey, particularly relocatory niche construction, seems to have increased in steps during the Devonian and again in the Cretaceous, with an expansion since the Cretaceous [22]. Bioturbation of marine sediments seems to have increased in two steps during the Cambrian, increased through the Palaeozoic, with a marked decrease during the Permo–Triassic boundary, and increased since the Cretaceous, particularly with the spread of many marine mammals who disturb the sediment. The thickness and persistence of shell beds seems to have increased in the Ordovician, the early Mesozoic and the Late Cretaceous, with substantial impact on the nature of soft sediment marine communities.

These are predominantly suspension feeders, such as stalked echinoderms, many articulate brachiopods and bryozoans (the dominant taxa of Palaeozoic marine benthic communities). In the face of such bulldozing, survival will be favored by increased body size (harder for bulldozers to displace), mobility (organisms can right themselves after disturbance) and a density of individuals (also harder for bulldozers to disturb). Bulldozing groups arose in the Cambrian but the number and diversity of such clades increased substantially during the Mesozoic Marine Revolution with the rise of echinoids, a variety of arthropod groups, burrowing gastropods and bivalves, in addition to skates and rays [22]. Predation also increased during the Mesozoic (252–66 Ma), driving siphonate bivalves and other burrowing organisms into the sediments for protection, further increasing bioturbation. In the Late Cenozoic (23 Ma–present), marine mammals, particularly walrus, have had a major impact on sediment disturbance [23]. Burrowing does not necessarily destroy the habitat of epifaunal organisms, however. Infaunal or semi-infaunal suspension feeders use the substrate as a home, rather than as a reservoir of food, and consequently stabilize the sediment as they modify it. Similarly, the sediment-binding activities of animal mucous, diatoms and bacteria can ameliorate the disturbances of burrowers [24].

Bulldozing is not limited to the sea. Large terrestrial herbivores have substantial effects on the physical structure of plant communities [25,26], not by eating them but by disturbing the habitat in their search for food. Such disturbances range from impacts on soil structure by burrowing mammals to the large-scale restructuring of plant ecosystems by elephants and other large herbivores. For example, the classic climax forests of the northeastern USA only exist because of the extinction of mammoths and mastodons some 12 000 years ago [27]. Prior to the disappearance of these massive (in both size and impact!) ecosystem engineers, the forests were open and more park-like rather than closed.

The increases in shell-bed thickness and in the burrowing and bulldozing by both marine and terrestrial animals are examples of increases in ecosystem engineering over evolutionary timescales, indeed, over hundreds of millions of years. But are these simply spillovers or the result of active selection?

From ecosystem engineering to niche construction

In considering the evolutionary implications of ecosystem engineering, Odling-Smee and colleagues introduced the concept of ecological inheritance [3] (Box 1) and suggested that persistent modifications to the environment such as those covered by ecosystem engineering will change the selective environment, influencing subsequent evolution of the niche constructor. However, in their view, niche construction results from the genetically informed, active, phenotypically plastic behavior of populations of organisms [3]. Although bulldozing fits this criterion, the formation of shell beds might not. Hence, I argue that ecosystem engineering and niche construction should be operationally distinguished as separate processes.

Escalation

One macroevolutionary pattern that illustrates the challenges of linking ecosystem engineering to niche construction is the long-term dynamics of interactions between predator and prey: the pressure for prey to relocate to avoid predators. The ability to relocate to avoid a change in the environment is one of the categories of niche construction [3]. Such relocation niche construction forms a crucial component of Vermeij's escalation hypothesis [28]. Escalation involves a response between predator and prey, leading to increasing adaptiveness within lineages. For example, among cephalopods, internal shells appear in the

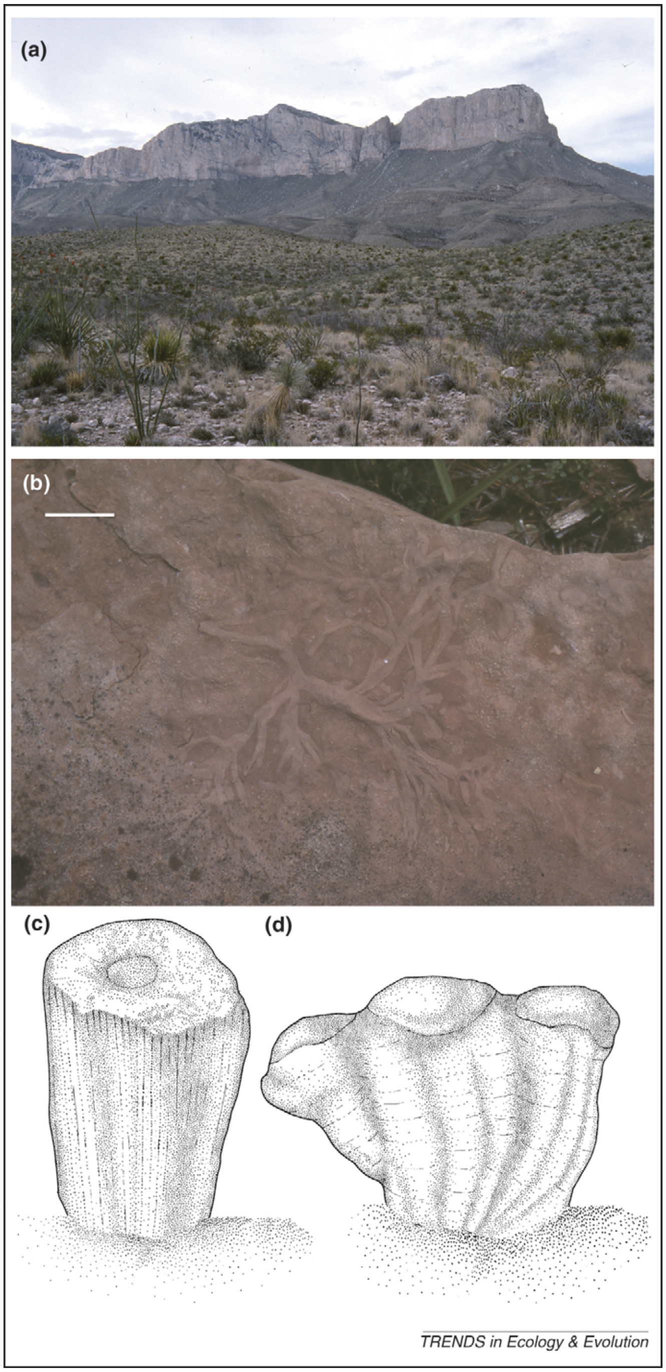

Figure 2. Examples of ecosystem engineering from the fossil record. **(a)** The Permian reef complex of the Guadalupe Mountains in west Texas (USA), a massive build-up of coralline algae, sponges, bryozoans, brachiopods and other groups. **(b)** Network of burrows showing the extent of bioturbation in the Lower Cambrian (Tommotian Stage) of Siberia. Plan view; scale bar = 1 cm. **(c)** and **(d)** Drawings of Cretaceous rudist bivalves, the dominant reef constructors of the Cretaceous. (c) *Barrettia* sp. (d) *Chiapasella* sp. Photos by D. Erwin. Drawings by M. Parrish.

Early Devonian (416–397 Ma), enabling a faster flight response, whereas Palaeozoic shelled nautiloids display adaptations for increased speed. Vermeij noted that escalation evidently occurred in bursts, punctuating longer periods of stasis. Escalation seems to have been particularly high during the mid-Palaeozoic, Cretaceous and later Cenozoic (e.g. Ref. [29]) (Figure 1). Paleontologists have not evaluated these bursts as niche modification but, as detailed by Vermeij and others, they are clearly long-term, macroevolutionary modifications of the niches of organisms.

Testing the operation of selection via ecological inheritance in a macroevolutionary setting poses significant challenges because paleontologists must infer process from pattern. Although Odling-Smee and colleagues have identified some valuable tests for niche construction [3], and some of the comparative tests can be applied to the fossil record, in many cases it will be difficult (if not impossible) to reliably distinguish between niche construction and Dawkin's 'niche changing'. Not all types of escalation involve niche construction, however, and this provides a means to test the relative importance of niche-constructing escalation versus non-niche-constructing escalation on diversity. For example, increasing armor and other predatory defenses among gastropod lineages confronted with shell-crushing crabs is not niche construction, whereas Odling-Smee and colleagues would consider the streamlining of gastropods to be niche construction.

Determining whether examples of ecosystem engineering are truly cases of niche construction is more challenging, particularly in the construction of shell beds or in bulldozing, where many taxa, often from evolutionarily distinct clades, contributed. Selection on individual species thus becomes quite diffuse and its significance difficult to gauge. An important issue that further complicates the understanding of deep time niche construction is whether the occupation of an engineered habitat is purely facultative, with the species involved also usually occupying other spaces, or whether it is obligate, particularly in cases with persistent ecological inheritance [30]. This might well change over the history of a clade, further complicating the analysis. Even where occupation is facultative, the existence of engineered habitats could have an important impact on abundance, buffering species during environmental perturbations. One intriguing aspect for future exploration is the role of ecosystem engineering in survival and recovery during mass extinctions.

Ecosystem engineering and diversity

Shell-beds, bulldozing and escalation each increase ecosystem engineering through the Phanaerozoic. Bulldozing and escalation, however, can have both a positive and a negative impact on diversity. Burrowing changes the geochemistry of sediments and provides a rich, three-dimensional habitat, but can destroy the habitats of epifaunal organisms. Similarly, large herbivores increase disturbance rates. Increased predation drives co-evolutionary responses with prey and can increase some types of niche construction. Whether the result of these changes on Phanaerozoic diversity is positive or negative is unknown, but ecological studies have established that, over the long-term, ecosystem engineering can have a positive impact on diversity by constructing habitats that can be occupied by other species, usually through increasing structural heterogeneity and patchiness and by direct impacts on resource availability (e.g. Refs [5,30]). Some of these effects are localized, as with mussel beds [31] and oysters [32], but, on balance, the cumulative long-term effect of increased environmental heterogeneity is likely to have had a net positive increase on diversity. In other words, diversity begets diversity and, as ecosystem engineering creates habitats for other species, particularly those than engage in further engineering, positive feedback ensues. The relationship between ecosystem engineering and diversity needs to be addressed both by theoretical modeling studies and by empirical studies that track ecosystem engineering within the same environment to determine the net effect.

Ecosystem engineering and innovation

Major innovations create new habitats for other organisms, in effect, increasing the carrying capacity of the environment. Have increases in ecosystem engineering and niche construction had an important role in generating these increases in carrying capacity during evolutionary innovations? Beyond the examples described here, the effects of mangroves, which arose ~120 Ma in the Late Cretaceous [33] and act as nurseries for coral reef fish [34], the spread of kelp and sea grasses, which baffle soft substrates, and the climatic and shading effects of forests on the understory all influence diversity. Thus, the notional carrying capacity of a system is also a function of the extent of these niche-creating activities, and actual diversity reflects the abilities of incumbents or immigrants to take advantage of them. Much of current evolutionary theory focuses on competition, a legacy of the influence of Malthus on Darwin, and on predation. The influence of positive interactions such as symbiosis has been appreciated more recently [35], but, in most cases, network effects of positive feedback have not been accounted for by evolutionary theorists [36]. Many palaeontological studies of diversity assume a logistic growth model, despite little evidence that such models apply at the level of multi-population species or communities, much less at the global level [37]. Even within such a framework, the crucial question is how carrying capacity grows. Do ecosystem engineering and niche construction provide sufficient positive feedback to increase carrying capacity?

But such a conceptual framework is itself deeply flawed because carrying capacity is an exogenous variable within the model. In other words, carrying capacity assumes that the system is in equilibrium and that no innovations will be introduced. Neither assumption is valid on evolutionary timescales. Understanding the growth regulation of biodiversity requires the development of models that eliminate exogenous variables, such as carrying capacity, but

Box 2. An economic view of innovation

Economists are as concerned with issues of growth as evolutionary biologists are, but they have approached the issue from a different perspective, and some of their insights could prove useful in understanding patterns of evolutionary innovation. Solow established that economic growth requires technological innovation: in the absence of innovation, growth eventually stalls [49]. Unlike biologists, who continue to be in thrall to Malthus, economists have not relied on logistic growth models and have no expectation of a carrying capacity. Rather, research over the past several decades has focused on the development of endogenous growth theory, whereby limitations to growth come out of the equations rather than being imposed externally (exogenously), as is the case with a carrying capacity.

Perhaps the greatest recent advance in this area was by Romer [38], who built upon earlier work and distinguished between goods that vary in their degree of rivalry and their degree of excludability. Rivalrous goods are those for which, if someone else uses the good, it degrades the ability of others to use the good. For example, there is a limit to how many can use a bicycle simultaneously. Non-rivalrous goods include global positioning system (GPS) signals or computer software, for which any number of simultaneous users is possible. The concept of excludability is subtly different because it relates to the ease with which a user can be excluded from using a good. An iPod®, for example, is an excludable good, fish in the sea or the concept of the calculus are not (Figure I). Romer's crucial insight was to realize that economic growth ultimately depends on the generation of non-rivalrous, non-excludable goods because these goods produce economic spillover effects (positive feedback) that percolate across the economy. These goods have a greater impact on growth than other types of innovation.

Romer's insights seem to me to be equally applicable to biology: the crucial innovations for the increase of biodiversity are those that have the greatest spillover effects on other organisms, and are closest to being non-rivalrous, non-excludable goods. Those with longer persistence will have correspondingly greater macroevolutionary impact. Oxygen is perhaps the paradigmatic example of a non-rivalrous, non-excludable good, whereas space on the intertidal zone serves as a useful example of a rivalrous, highly excludable good. This economic insight indicates that the greatest impact of niche construction and ecosystem engineering is when they produce innovations that are analogous to non-rivalrous, non-excludable goods with long persistence.

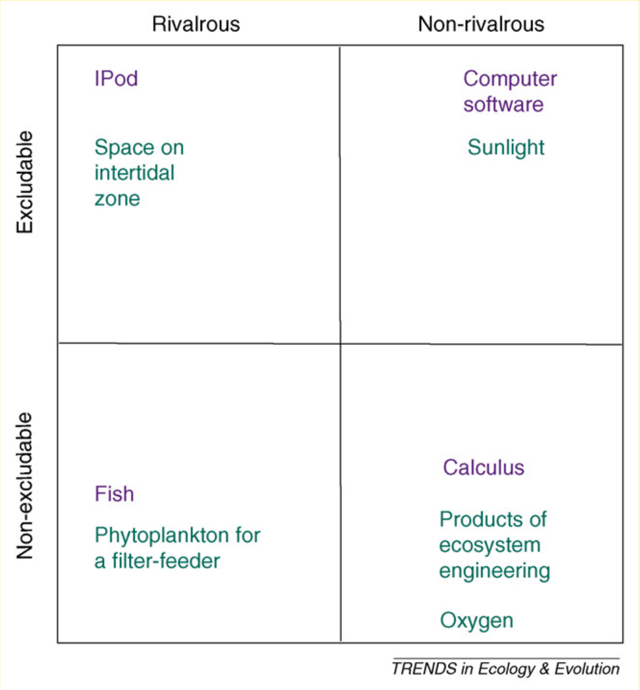

Figure I. The division of economic goods into rivalrous versus non-rivalrous and excludable versus non-excludable goods is equally useful for understanding the potential diversity impact of different biological innovations. Rivalrous goods are those that can have only one user at a given time, whereas non-rivalrous goods are those that can have multiple users without degrading the good. In a biological sense, this maps to goods for which there is competition (rivalrous) versus those for which there is little competition. Subtly different is the distinction between excludable and non-excludable goods, which differ on the extent to which it is easy to exclude others from using a good. The goods listed in purple are examples of economic goods in each category, and the goods in green are biological goods.

incorporate critical factors. Understanding and accounting for these feedback mechanisms will require empirical approaches designed to identify them, informed by modeling studies. Of particular value will be insights from network dynamics, where a rich toolkit for understanding positive and negative feedback already exists.

Economists have been engaged in a struggle to understand economic growth over the past several decades, eliminating exogenous variables and puzzling out network effects (Box 2), and there are sufficient similarities between the problems of economic and evolutionary growth to indicate that some insights from the economic growth theory might be useful for biology. Understanding biodiversity requires models in which growth reflects both evolutionary innovations and the attendant construction of new niches. Ecosystem engineering and niche construction encompass a range of spillover effects, whereby the initial adaptation benefits a range of other taxa. As Romer recognized for economic growth [38], spillover effects seem likely to have had an important role in the growth of biological diversity. However, some engineering effects seen to have had a greater impact on diversity. The origination of oxygenic photosynthesis is the paradigmatic example of a non-rivalrous, non-excludable effect (see Box 2): after the oxidation of the atmosphere ~2.4 billion years ago and more substantial oxidation of the oceans and atmosphere 550 million years ago, the resulting change in the environment was pervasive, created enormous evolutionary opportunities for oxidative metabolism and created a resource, the use of which was, in most settings, close to density independent. Similarly, the effects of bioturbation on the diversification of animals during the Cambrian were probably substantial, although much work remains to be done to establish the extent of the contribution. Thus, ecosystem engineering seems to be the most plausible source of spillover effects with sufficient breadth to have a major impact on diversity. In this view, evolutionary innovations that create engineering opportunities with substantial spillover effects generate the greatest number of new niches and have the greatest impact on biodiversity. But there is a continuum of spillover effects from this extreme to strict niche construction, producing fitness advantages primarily for the focal species, and on to adaptations that generate no ecosystem inheritance and, thus, have no spillover effects at all.

Conclusions

Several measures of ecosystem engineering, including shell beds and bulldozing, indicate that engineering has increased through the Phanaerozoic with Cretaceous and Modern ecosystems displaying considerably more ecosystem engineering than did the Palaeozoic. The increased ability of some prey to flee predators also indicates an increase in niche construction, and thus the growth in ecosystem engineering might also indicate increased niche construction. I argue that such positive feedback is ecologically and evolutionarily significant, although how much of diversity is attributable to such feedback is unclear. Understanding the role of positive feedback in generating diversity is an important challenge for paleontologists and other evolutionary biologists. One study of ecological facilitation in intertidal marine communities indicated greater facilitation in tropical and warm temperate communities than in higher latitudes [39]. Is this generally true of ecosystem engineering? Is there a similar macroevolutionary biogeographic variation in ecosystem engineering? If so, it should be expected that latitudinal diversity gradients – a subject of considerable interest – in part, reflect different magnitudes of engineering and niche creation. Can we develop models in which ecosystem engineering and even niche construction are endogenous components of changes in diversity?

There are also other challenges. Paleontologists have documented a wide range of migrations in the fossil record, using techniques as varied as traditional biogeography, phylogenetic methods and, more recently, genetic markers in living taxa [40,41]. Less studied are the paleoecological effects of such introductions. Yet many recent invasions have been accompanied by substantial ecosystem engineering effects [7]. If ecosystem engineering is implicated in evolutionary innovations, this naturally raises the question of whether it has been involved in the rebuilding of ecosystems in the wake of biotic crises ranging in scale from climatic and sea-level change to the great mass extinctions. How have these processes influenced community assembly and recovery from mass extinctions? Have they had a significant role in evolutionary innovations? Are ecosystem engineers more resistant to extinction? Has the absence of ecological inheritance inhibited recovery after biotic crises? There are many exciting challenges for future work.

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