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Opinion

# 'Earth system engineers' and the cumulative impact of organisms in deep time

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**Understanding the role of humans as 'ecosystem engineers' requires a deep-time perspective rooted in evolutionary history and the fossil record. However, no conceptual framework exists for studying the rise of ecosystem engineering in deep time, requiring us to consider effects that fall outside the scope of traditional definitions. Here, we present a new framework applicable to both modern and ancient engineering-type effects. We propose a new term – 'Earth system engineering' – to describe biological processes that alter the structure and function of planetary spheres, and which combines core tenets of ecosystem engineering, niche construction, and legacy effects. We illustrate this framework using the fossil record, and show how it can be applied across the tree of life, and throughout Earth history.**

## Highlights

Over ~3.5 billion years our planet has become increasingly bioengineered, leading to stronger biotic controls over the distribution and flow of resources, and the character of ecological niches. Taxa that have oversized effects in this regard are called 'ecosystem engineers'.

By focusing on processes, rather than organisms, we can extend the concept of ecosystem engineering ('EE') to include the full temporal and taxonomic extent of Earth history.

The consequences of many human EE processes are contributing to the biodiversity crisis. However, answering the question 'are we unique?' requires reconstructing the history of EE, and therefore a new framework that can be also applied to deep time.

By integrating modern and deep-time engineering processes, we offer a framework to assess whether human EE activities (and consequences) have parallels in Earth history, or if our impact on the biosphere is really unprecedented.

## The cumulative global impact of ecosystem engineering on geological timescales

Ecosystem engineers are organisms that modulate the availability of resources to other species by causing physical state changes in biotic or abiotic materials. In doing so, these organisms modify, maintain, or create habitats, and have significant impacts on the abundance and identity of species within the ecosystem [1] (Figure 1). The concept of species as ecosystem engineers has become widespread in ecology [2,3], and crucial to understanding the structure and function of the biosphere [4]. There has also been much discussion surrounding the role of humans as ecosystem engineers [1,5,6] (Figure 1), raising the questions: are human engineering activities unique in Earth history, and are the consequences of these activities predictable? Answering these questions requires searching the fossil record for intervals where new engineering processes have emerged, and assessing how these have impacted the biosphere. However, there is no unified conceptual framework for studying ecosystem engineering in deep time. Creating one poses conceptual challenges, and requires us to consider aspects outside the scope of traditional definitions.

Here, we propose a framework that combines both shallow and deep-time perspectives. First, we erect a new term to describe engineering processes that not only modulate biologically important resources, but also alter the structure, function, and/or interactions between **planetary spheres** (see Glossary). To distinguish these, we propose the term 'Earth system engineering' ('ESE'). Second, we describe a spectrum of scenarios surrounding the evolution of new ecosystem engineering (EE) and ESE-type effects. Lastly, we use case studies to show how these can be broadly applied both across the tree of life and throughout the span of Earth's history.

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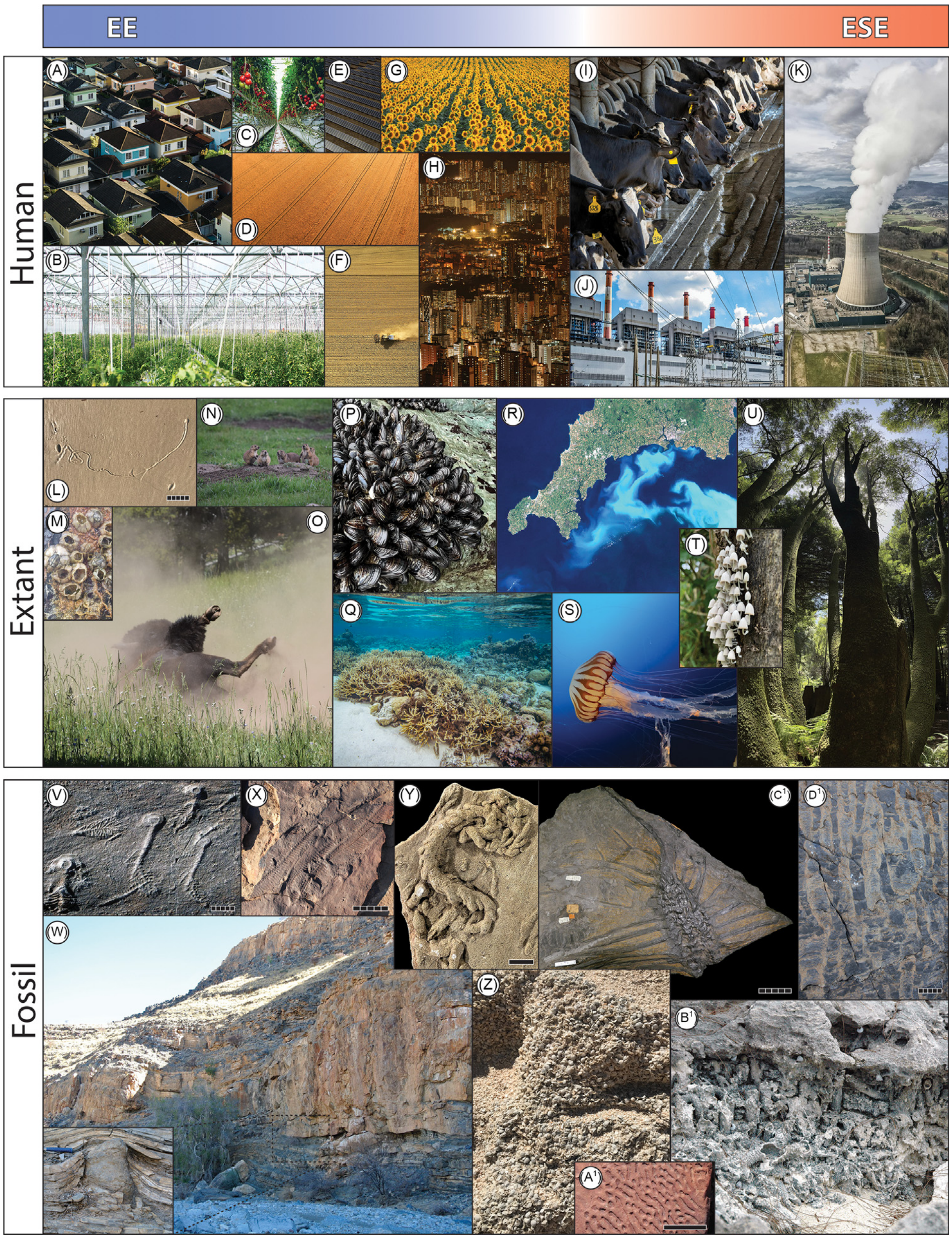


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Figure 1. A compilation of engineers – and engineering processes – recognized in humans (top panels), non-human organisms (middle), and in the geological record (bottom panels), and arranged on a spectrum of ecosystem engineering ('EE') to Earth system engineering ('ESE') processes/consequences (for panel explanations see S1 in the supplemental information online). We argue that understanding the role and impact of humans as ecosystem and Earth system engineers – in particular to what extent we are unique, and what specifically makes us unique – requires the fossil record and a synthesis of engineering-type effects throughout Earth history. Our proposed framework is designed to fulfill this role. Scale bars in panels L, V, X, Y, A', and C' show 1 cm increments.

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## EE versus ESE

Many of the EE examples originally defined by Jones *et al*. [1] were inherently local or regional in spatial scale, with impacts ranging in temporal scale from ephemeral (i.e., disappearing with the organism upon death) to 1000's of years. However, the fossil record preserves evidence for biological processes that had global impact, induced permanent step-changes in **Earth systems**, and in turn permanently influenced the biosphere [7,8]. The emergence of **oxygenic photosynthesis** >2.4 Ga is a clear example, raising the concentration of a crucial resource ($O_2$) which in turn facilitated the emergence of multicellular eukaryotes [9,10]. Although, for brevity, Jones *et al*. [1] focused on physical engineering (while acknowledging the existence of other types, such as chemical and transport engineering), oxygenic photosynthesis changes resource availability, influences energy flows, and controls the distribution of habitable space for a broad swathe of life. Consequently, attempts to synthesize how stepwise evolutionary innovation has influenced the history of life should include these processes [3].

We propose the term 'Earth system engineering' to describe biological processes that alter chemical, physical and/or functional characteristics of the Earth, and alter resource flows on a planetary scale. Given that most engineering-type effects are not limited to a single species, we focus on processes rather than individual taxa. As a result, we refer to ecosystem engineering (EE) and Earth system engineering (ESE), and ecosystem engineers (EEs) and Earth system engineers (ESEs) when referring to the responsible organismal groups. In our definition, ESE is characterized by having global-scale consequences that often persist on geological timescales ('intermediate' and 'long term' categories identified by Mángano *et al*. [11]), and which can impact biota that do not necessarily coexist with the engineers in space and time. Thus, ESE has globally distributed and long-lasting legacy effects that can affect macroevolutionary dynamics (see also [4,7]). In many respects this definition combines two other concepts: '**niche construction**' [12,13] and '**legacy effects**' [14]. However, we argue that the scale and persistence of some engineering processes are better described as influencing the character and interactions between planetary spheres – resulting in permanent (and cumulative) step-changes in Earth system structure and function – and operating on larger scales than envisaged by either term. Capturing the interplay, evolution, and persistence of biological modification also requires moving beyond purely physical ecosystem engineering to include chemical, biogeochemical, energetic, and climatic effects as well. Defining 'Earth system engineering' in this way allows us to consider engineering-type effects in deep time, and how these engineering impacts have contributed to overall habitability (see also [15]).

## Characteristics of ESE

ESE influences global environments, including those that the engineers themselves do not necessarily inhabit. This can arise in different ways. ESE processes that influence resources involved in biogeochemical cycles, operating in the atmosphere and hydrosphere, and with long residence times are more likely to influence taxa in other spatially distant ecosystems. For example, marine **calcium carbonate ($CaCO_3$) biomineralization** involves the sequestration of calcium from seawater, and $HCO_3^-$ (which is linked to atmospheric $pCO_2$ via ocean dissolved inorganic carbon (DIC) chemistry), in order to produce $CaCO_3$ skeletons. The skeletons themselves are associated with several EE processes, ranging from hydrodynamic baffling, substrate modification, and habitat creation (e.g., as reefs). However, on broader scales biomineralization also has global consequences – for example, as a major contributor to the deep-sea sediment sink for atmospheric $CO_2$ (via augmentation of the export production part of the **biological pump**, or due to its role in the carbonate-silicate geochemical cycle [16]) – and thus qualifies as an ESE process. ESE processes may also achieve global-scale impacts by modulating some factor of the climate and its energy budget. For example, plant coverage can have ESE consequences through **vegetation-albedo feedbacks**, thereby impacting the planet's climate on a global scale [17–19]. The evolution and spread of Paleozoic forests thus would have had particularly large impacts on the Earth's climatic energy budget, as increased canopy coverage lowered albedo and increased thermal energy maintained at the Earth's surface [20].

## Glossary

**Bacterial methanogenesis:** an anaerobic metabolism generating ATP via synthesis of methane, commonly through the reduction of carbon dioxide with hydrogen.

**Biological pump:** the process by which atmospheric inorganic carbon is fixed into organic matter via photosynthesis, and sequestered into the deep ocean via sinking and decomposition. Thus, the biological pump has the potential to be a large feedback mechanism within the climate system.

**Biomineralization:** the process by which living organisms produce minerals, often resulting in robust mineralized tissues or structures (e.g., mollusk shells, reef frameworks).

**Body fossil:** the remains of organisms preserved in the fossil record (e.g., bones, shells, leaves). By contrast, trace fossils record organismal behavior, movement, and/or biological activity (e.g., trackways, burrows etc.).

**Calcium carbonate ($CaCO_3$) biomineralization:** the sequestration of calcium/carbonate ions from the seawater to create $CaCO_3$ skeletons. In the presence of adequate nucleation sites, $CaCO_3$ precipitation is governed by the concentrations of calcium, dissolved inorganic carbon (DIC), and pH.

**Castorids:** members of the rodent family Castoridae, which contains two living species of beavers (*Castor fiber* and *Castor canadensis)* and their extinct relatives. These dam-builders are the most frequently used example of ecosystem engineers.

**Earth systems:** an approach to studying Earth history that defines the planet as a group of interacting, interrelated, or interdependent parts (systems) that work together to form a complex whole. Systems include: the atmosphere, hydrosphere, geosphere/lithosphere, biosphere, cryosphere, and pedosphere.

**Legacy effects:** the engineered aspects of the environment, and the processes/consequences of engineering that are still in effect when the engineers themselves are dead or absent.

**Niche construction:** the abiotic and biotic modification of the environment by living organisms, and their resulting changes to ecological and natural selective pressures.

Similarly, by operating on long timescales, ESE processes often have consequences that exist beyond the lifetimes of the engineers (and that are distinct from EE processes). For example, the engineering impacts of mollusks as producers of shell pavements can be long-lasting [4,21], but only on local- to regional-scales where these shell beds form. Rather, the temporal scale of a spatially widespread process depends on the persistence of the ESE in different populations through time, as geologic feedbacks may balance out any ESE-driven perturbance to the global system. For example, atmospheric $CO_2$ levels that are currently elevated through the burning of fossil fuels – a current human ESE process – will eventually decline in our absence on geologic timescales, via continental weathering balances [22]. ESE processes can also have surprisingly short legacy effects, particularly chemical species with short residence times (e.g., methane).

We also note a mismatch in taxonomic resolution between organisms that perform EE versus ESE processes. Specific EE processes can be associated with either a single genus, and for limited intervals of geological time (e.g., dam building by **castorids**, dating back to Miocene [23]), or by families, orders, or even broader clades that have performed the same role over millions of years (e.g., metazoan reefbuilding [8,24]). In contrast, organisms we define as ESEs tend to have coarser taxonomic scale, distributed amongst polyphyletic groups that may only be united by a common body plan, threshold body size, behavior, or metabolism. The distribution of oxygenic photosynthesis within single-celled groups (see [10,25]) is one example. To the best of our knowledge, there is no single species, or genus, we can identify that is solely responsible for an ESE process, with the possible exception of *Homo sapiens*. Lastly, an interesting corollary of our definition is that the majority of our ESE processes involve a fundamental state change in the resource of interest, or its movement from one reservoir into another such that it becomes bioavailable to a new suite of organisms (for example, the fixation of carbon, or nitrogen in soils).

In summary, ESE processes are distinct from EEs on the basis of their consequences for biota at global scales – including in locations, environments, and realms that the engineers do not inhabit – through their influence on nutrients and/or resources that have planet-wide distribution (and circulation). In many other aspects, however, EEs and ESEs show substantial overlap, for example in the temporal duration of legacy effects, the spatial distribution and/or abundance of organisms responsible, and the taxonomic scales with which processes are associated.

## Timing and thresholds

Extending EE and ESE concepts into a deep-time context allows consideration of two additional aspects that have not been discussed in the strict ecological literature, principally: (i) timing (i.e., when, and under what circumstances, does an EE/ESE process emerge?), and (ii) thresholds (can EE processes become ESE processes, and vice versa?) (Box 1). Building from previous work [1,3], we distinguish between process and consequence, recognizing that one process can have multiple consequences.

### Timing

Among the simplest of scenarios is that an EE/ESE process is initiated immediately with the emergence of a new trait or behavior, and this immediately leads to one or more consequences (Box 1). When multiple consequences are associated with a single process, some consequences may appear only once the process becomes more prevalent through time with the geographic expansion (and/or evolutionary radiation) of the taxonomic group. A more complicated scenario involves a temporal 'lag' between processes and consequences. In this case, an EE/ESE process arises after the emergence of a new trait, and the associated consequence(s) are only initiated after the organism, or behavior, reaches an abundance, geographic, or activity-based threshold (e.g., the increasing diversity of diatoms and their role in the formation of biogenic siliceous sediments

**Oxygenic photosynthesis:** the metabolic process in which carbon dioxide and water are synthesized into carbohydrates and oxygen using light from the sun. This umbrella term covers the means by which plants, algae, and cyanobacteria generate oxygen.
**Planetary spheres:** interacting, interrelated, or interdependent parts of the Earth system that work together to form a complex whole. See 'Earth systems' above.
**'Pull of the recent':** a consequence of three factors that may artificially create the marked increase in diversity documented within the Cenozoic, including more complete sampling in the recent, misattribution of fossils to recent taxa, and better taxonomic/phylogenetic understanding of extant taxa.
**Silica biomineralization:** the process by which living organisms (diatoms, sponges, plants) produce silica minerals within cell walls or intracellularly in various cell types. In marine systems silica biomineralization by diatoms plays an important role in both the silicon and carbon cycles, particularly via the biological pump.
**Vegetation-albedo feedback:** modification of the climate system through the presence of vegetation, due to the resulting changes in albedo (i.e., darker color and lower albedo of dense vegetation relative to snow, or the lighter color and higher albedo of dense vegetation relative to soils).

[26]). The threshold controlling lags between consequence and process may also be modulated by extrinsic environmental factors, such as the climatic variables that control silica cycling and biosediment diagenesis [26]. Lastly, an EE/ESE process and consequence may disappear, only to reappear in similar form after an interval of time. The consequence may persist for some time after the cessation of the process, creating a 'legacy effect' [14] on timescales ranging from seconds to millions of years. Although this model may apply to individual species – for example, blooms of biomineralizing invertebrates, which provide substrates for other organisms [27] – it also applies to ecological communities. Arguably the best example is reefs over mass extinction events, which can disappear, or become severely reduced, for millions of years [28]. In this example, although the EE consequences before and after extinction can be similar, the organisms making up the communities are different, particularly over extinctions with outsized ecological impacts (discussed in detail in Box 2).

## Thresholds

The fossil record preserves numerous examples of a single process driving both EE and – once a threshold is reached – additional ESE consequences (Box 1). Alternatively, as a single process becomes more widespread and/or intense through time, this can potentially result in an EE consequence becoming 'upgraded' to an ESE consequence (e.g., the evolution of oxygenic photosynthesis). Hypothetical trajectories that EE processes might take in becoming ESE processes

### Box 1. Timing and thresholds

We can hypothesize timing- and threshold-related scenarios for the onset of Ecosystem engineering ('EE') and Earth system engineering ('ESE') processes/consequences, and link these to specific examples.

#### Timing

An EE process may lead to one (A) or more (B) consequences (Figure I). For example, in metazoan reefs individual bioherms baffle currents and create hydrodynamic refugia. However, with continued growth reef structures can influence the distribution of sediment types and associated communities along coastlines [24]. The EE process may also substantially precede the onset of consequences, creating a macroevolutionary lag (C); for example, **silica biomineralization** in diatoms. Diatoms had low abundance throughout much of the Mesozoic, but rose to prominence in the Late Cretaceous and began forming extensive seafloor siliceous oozes [26,40]. Finally, EE/ESE processes and consequences may disappear and reappear (D) with the changing abundance of organismal groups (E). For example, reef tracts have disappeared or become severely reduced for millions of years following extinction events [28] (see also Box 2), only to return (albeit with different framebuilders) following recovery.

#### Thresholds

A process may drive different EE and ESE consequences. For example, metazoan bioturbation ventilates marine substrates on local scales, creating habitable ecospace (EE) [11]. However, sufficiently widespread bioturbation can cross a threshold (F), and also influence global biogeochemical cycles (ESE) [8,41]. Alternatively, an EE process can become an ESE over time (G). For example, oxygenic photosynthesis initially created conditions that fostered the rise of aerobic microbial metabolisms on extreme local scales [42]. However, following the Great Oxidation Event an increasingly oxygenated atmosphere altered global biogeochemical cycles, weathering cycles, and facilitated the rise of animals (see discussion in [43]). Conversely, an ESE can be reduced to an EE (H). For example, bacterial methanogenesis warmed the Hadean-Paleoarchean atmosphere [35,44], allowing life to exist away from hydrothermal vents (ESE). With the rise of other microbial metabolisms, however, methanogens likely became restricted to marginal environments that stayed anaerobic, and now play a role in supporting methanotrophic communities (EE).

Finally, negative (I) and positive (J) feedbacks may be crucial. For example, planktonic $CaCO_3$ biomineralization captures carbon and exports it to the seafloor via the biological pump (ESE), but also creates calcareous seafloor substrates (EE) [40]. Separately, anthropogenic $CO_2$ leads to ocean acidification (ESE), decreasing the abundance of calcareous phytoplankton [45] and their effectiveness as a carbon sink [29,46]. Conversely, there exist positive feedbacks (facilitation – 'F') where new and pre-existing processes interact to enhance a consequence (J). For example, on small scales, methanogenesis supports the gut microbiomes of mammalian herbivores (EE). However, large-scale animal husbandry in the last ~5000 years has enhanced methane emissions, becoming a significant component of anthropogenic warming (ESE) [47,48].

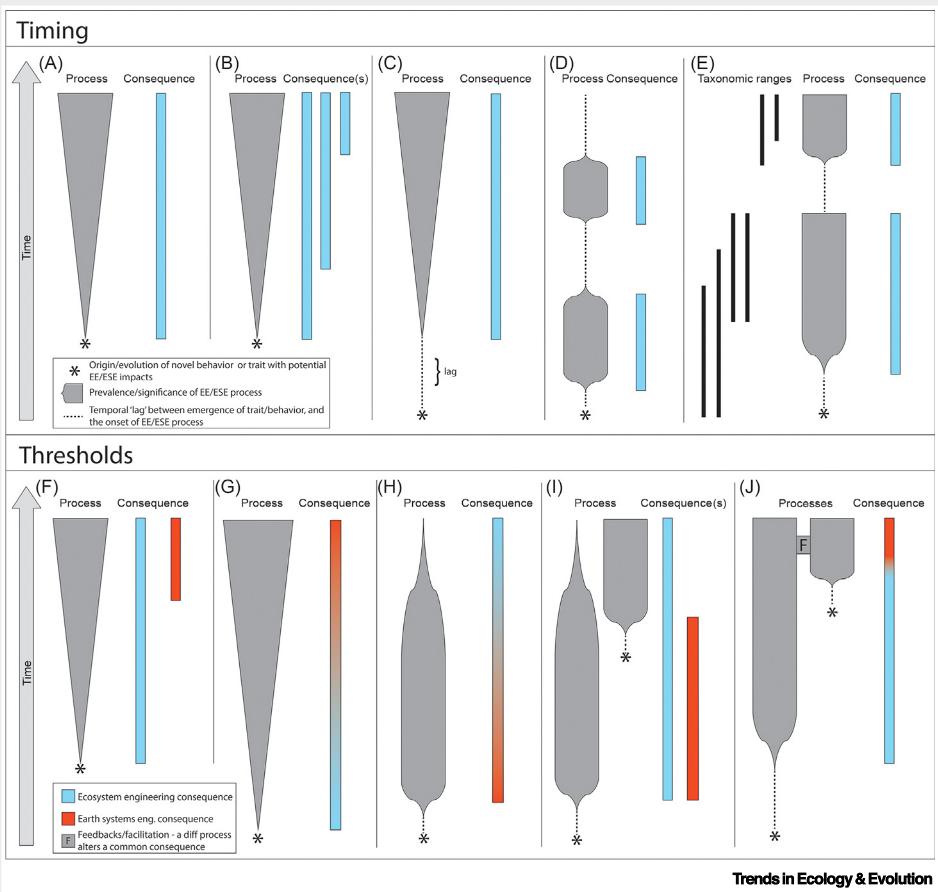


Figure I. Key concepts involved with extending aspects of timing (top panel) and thresholds (bottom panel) in engineering-type effects into deep time. Blue bars represent the presence of ecosystem engineering (EE) consequence(s) and red bars indicate the presence of Earth systems engineering (ESE) consequences through time. In this framework, processes are depicted as spindles spanning the temporal range of the process, with widths expanding/contracting to reflect the prevalence or scale of impact. Both spindle length and width can be derived from quantitative or categorical data from the fossil record. In contrast, EE and ESE consequences are binary in this framework, only incorporating the presence or absence of evidence for change arising from the EE/ESE process. We show consequences as binary, because it is typically easier to quantify processes in the fossil record (e.g., bioturbation indices, reefal volume, depth of root systems etc.) than consequences, although modeling approaches [49] and global databases [50] show promise.

are illustrated in Figure 2. Conversely, as the prevalence of a process decreases through time, an associated consequence can be downgraded from ESE to EE. Although there are putative examples of this – for example, **bacterial methanogenesis** – these transitions appear to be much rarer. A third scenario involves feedbacks between different EE/ESE processes, and possible impacts on existing consequences. An example of this dynamic involves negative interactions between processes, such as the rise of anthropogenic $CO_2$ emissions, and resulting decrease in the abundance of calcareous phytoplankton (and thus the efficiency of the biological pump [29] – a vital biogeochemical process that captures atmospheric carbon and transports it to deep marine reservoirs. The final scenario involves 'facilitation', whereby the emergence of a new process generates positive feedbacks with a pre-existing process, in turn enhancing a consequence. In extreme cases, this raises the impact of the consequence from EE to ESE; one clear example is methane production (via bacterial methanogenesis) in mammalian herbivores, brought about via the development of large-scale animal husbandry in the last ~5000 years (Figure 2).

## Detecting EE and ESE processes in the geological record

The deep-time record of ecosystem engineering is preserved through both direct and indirect evidence, but also relies to some extent on inference (see also [30]). Direct evidence is preserved in the form of **body fossils** (i.e., the engineers themselves) – for example, fossil reef structures, shell pavements, and preserved root systems. Indirect evidence instead preserves a record of the process – for example, the burrows and other traces left by bioturbating organisms [11], some laminated sediments (the result of microbial mat growth), and traces of mechanical destruction, predation and bioerosion. In marine ecosystems these latter processes are a powerful control on rates of sediment production [31], and in terrestrial ecosystems an agent of afforestation, and habitat creation/destruction [32]. However, the recognition of many ancient EE/ESE processes also relies on inference, either through the interpretation of preserved fossil morphology (or paleotopography), or through geochemical/geological proxies where a biological driver is implied, but not preserved. In the former case, an example involves the reconstruction of feeding apparatuses in extinct invertebrates to track the origin and expansion of suspension feeding (e.g., [33,34]). In the latter case, the evolution of many powerful ESE processes (e.g., biological influence over the sulfur cycle) are commonly preserved in redox-sensitive trace elements or isotope records, which do not directly record either the process or the consequence, but rather the consequence by proxy. For intervals of deep time where the record is particularly poor – and thus

### Box 2. Case studies

Three case studies highlight our framework's utility in integrating the study of ecosystem engineering/Earth system engineering (EE/ESE) in taxonomically disparate groups, and through both shallow and deep time. The transpiration of water from leaf/stem surfaces is one of many EE/ESE processes carried out by land plants (Figure IIA), inferred globally based on transpiration-specific ecophysiological reconstructions of Pennsylvanian plant taxa and their estimated prevalence (see S2 in the supplemental information online). Glacial–interglacial cycles drove alternation between vast peat swamp biomes covering much of the tropics (dominated by lycopsids and sphenopsids) and drier ecosystems dominated by conifers. Higher transpiration rates [51] had ESE consequences, as peat deposition created important sinks for atmospheric $CO_2$ leading to glaciation [52] thereby increasing planetary albedo (Figure IIA). The magnitude of these processes and consequences were curtailed with the extinction of arboreous lycopods at the end of the Desmoinesian, and with the nearly global disappearance of this biome in the early Permian [53].

The process of urbanization is associated with numerous EE/ESE consequences (Figure IIB, left). Increasing states of urbanization (modified from Ellis [54]) include the development of temporary settlements, permanent settlements, roads, cities, and, eventually, concrete structures. Temporary aggregations of humans created refuse piles attracting commensal species and impacting soils, while the permanent aggregation of humans produced and destroyed habitat (EE). The development of roads and cities further fragmented habitats and created impermeable surfaces (EE). Finally, concrete structures created urban heat islands (EE) and contributed to atmospheric $CO_2$ production (ESE). The EE effects of urbanization in New Jiangwan Town in Shanghai, China (Figure IIB, right) show that habitat destruction and fragmentation, particularly declines in wetland area and connectivity, have led to decreased bird biodiversity (modified from Xu *et al*. [55]).

Reef communities are among the most important EEs in modern oceans (Figure IIC), creating three-dimensional habitat, performing vital biogeochemical functions, and hydrodynamically altering resource flows [56,57]. We quantify reef building EE processes through the Devonian-early Carboniferous, using the types of reef facies recorded in the geological record (see S2 in the supplemental information online). The Early to Mid-Devonian interval represents a Paleozoic apex in reef development [8,24,58]. Silurian patch reef structures evolved into more complex and extensive barrier reef systems built primarily by stromatoporoid sponges and tabulate corals in the Devonian, leading to the formation of associated forereef and lagoon environments (EE). During the Givetian, the geographic extent of reefs expanded, arguably leading to a new ESE consequence in the sequestration of substantial amounts of carbon in the sedimentary record [58]. By the mid-Frasnian, reef collapse associated with the Late Devonian Biodiversity Crisis reduced reefs to small-scale, microbial buildups lacking EE consequences beyond baffling/sediment binding [59]. Relatedly, rimmed carbonate platform morphologies disappeared, replaced by ramp morphologies with open hydrodynamics [60].

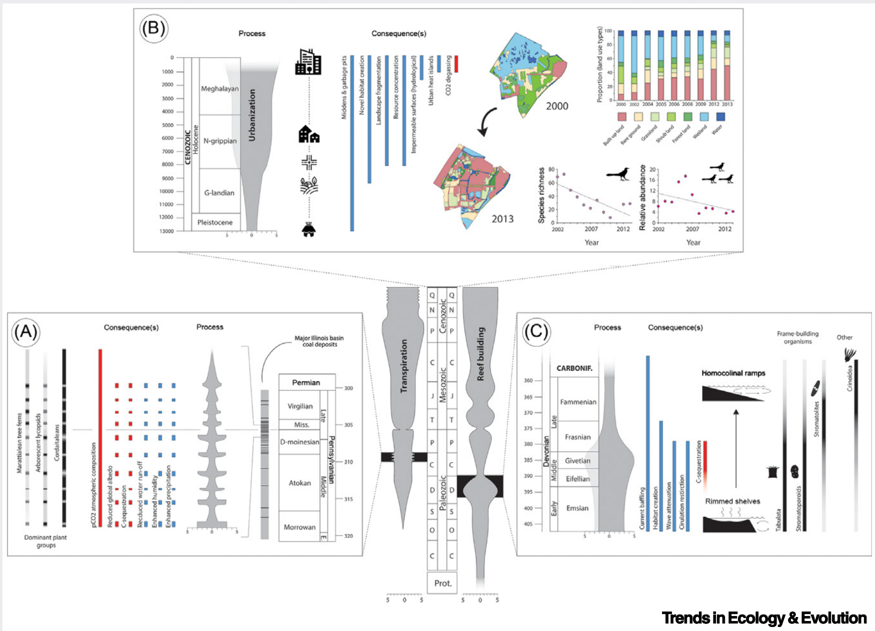


Figure II. Case studies illustrating the application of our new framework for studying ecosystem engineering/Earth system engineering ('EE'/'ESE') processes and consequences in deep time. The width of the spindle (gray) indicates changes in the prevalence or significance of the engineering process. Blue bars represent the presence of EE consequence(s) and red bars indicate the presence of an ESE consequence through time. Case studies include: (A) cycles in transpiration generated by equatorial swamp forests in the Carboniferous, (B) the rise of urbanization through human history, and (C) the decline of large reef systems in the Late Devonian.

## Outstanding questions

Are appearances of new EE/ESE processes distributed evenly throughout Earth history, or are they clustered in specific intervals of geological time? Answering this question will illustrate whether life's influence over Earth systems function has progressed steadily, or via a series of dramatic step-changes.

In the context of EE/ESE impacts, are humans unique as a species? Does our impact on Earth systems structure and function primarily stem from our abundance, distribution, generalist behavior, the rate at which we are modifying the environment, or – alternatively – our ability to harness multiple and new energy sources?

Are there other examples of emerging EE/ESE processes in Earth history that have led to mass extinction? Human activities have been unequivocally linked to the ongoing biodiversity crisis; however, are there other examples in deep time when the appearance of new EE/ESE impacts has led to intervals of rapid biotic turnover?

Alternatively, to what extent have these same EE/ESE processes led to new evolutionary opportunities on longer timescales?

geochemical proxies are rare – a final approach could rely on molecular dating of genes responsible for specific metabolic pathways. For example, Moody *et al*. [35] used an ancestral state reconstruction to establish that the last universal common ancestor 4.2 Ga was likely an anaerobic acetogen, and the resultant $CH_4$ and $CO_2$ would have been a powerful control on early Earth ecosystems.

Intuitively, these methods for detecting EE/ESE processes have a '**pull of the recent'** effect, whereby the engineering impacts of organisms emerging more recently – and thus having more readily interpretable behavior, biology, and a more complete fossil record – are more reliably reconstructed. For example, putative Precambrian animal fossils that may fall near the base of the metazoan tree frequently possess little morphology that can be identified through comparison with extant phyla. In these cases, their paleobiology and paleoecology are unknown, and thus their status as EEs/ESEs are enigmatic. Despite this, novel paleobiological techniques are allowing us to infer aspects of community structure that would likely have been involved in crucial EE processes (e.g., [36]), and so the record of engineering over ancient intervals in Earth history is coming into focus.

## Concluding remarks

The evolutionary history of ecosystem engineering presents a unique opportunity, allowing us to not only establish links between engineering processes and consequences, but also long-term ecological and evolutionary outcomes (see Outstanding questions). Erecting the term 'Earth

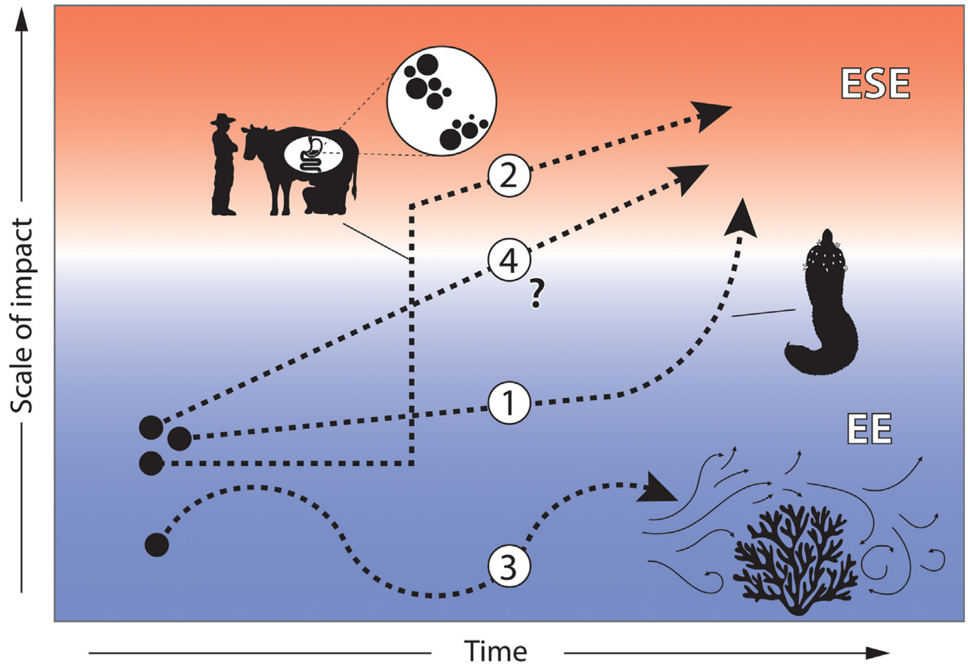


Figure 2. Conceptual figure showing hypothetical pathways through which ecosystem engineering ('EE') processes can become Earth system engineering ('ESE') processes, including: (1) the emergence or evolutionary step change in a trait that is responsible for producing an EE process, and which intensifies that process (e.g., the evolution of complex musculature allowing penetration into sediment and mixing); (2) ecological facilitation, whereby organisms interact in a way that enhances pre-existing EE processes and elevates them to an ESE (e.g., the rise and mass adoption of ruminant animal husbandry); (3) the strength of an EE process can wax and wane through time, without ever becoming an ESE process (shown here, current baffling at different stages of reef growth), and finally (4), a simple increase in population size and/or biomass until reaching a threshold. Note that although (4) is the simplest scenario, it is unclear whether it actually exists, and most well-studied examples follow one of the other, non-linear trajectories.

system engineering' allows us to consider interactions with the Earth system that are global in scale, and with legacy effects persisting for millions of years. Our framework also illuminates the successive behavioral, physiological, and anatomical innovations that have had a cumulative impact on nutrient flows on all spatial scales, thus 'bioengineering' the planet we live on. By extending ecosystem engineering into an evolutionary context, we can also ask whether the emergence of new EE/ESE processes are clustered in evolutionary history, and if they have predictable outcomes. Alternatively, the paleontological and geological records may also offer crucial data surrounding what happens when EE/ESE processes are weakened or temporarily absent – something that has been studied in the aftermath of mass extinctions [37,38], and is a growing concern in light of the ongoing biodiversity crisis [38,39]. Perhaps most importantly, however, this framework allows us to ask whether anthropogenic EE/ESE processes are unique in Earth history (Figure 1) – a question that we argue can only be answered using a multi-billion-year baseline, and a perspective that the fossil record provides.

**Author contributions**

All authors contributed to the development of the ideas, the conceptualization of the figures, and edited the manuscript. S.A. F.D. wrote the first draft of the manuscript and drafted the figures with input from M.M.C., A.T.C., and A.E.B. S.K.L., S.A.F.D., C.V.L., and P.J.W. obtained the funding for the working group meetings where these ideas were developed.

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## Declaration of interests

No interests are declared.

## Supplemental information

Supplemental information associated with this article can be found online at https://doi.org/10.1016/j.tree.2025.08.005.

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