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# Revisiting the geomorphological-biological divide: An introspective biogeomorphological perspective

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## Abstract

We suggest that biogeomorphology should challenge the traditional dichotomy between living and non-living components of Earth surface systems. To achieve this, biogeomorphologists should gain a better understanding of eco-evolutionary models and empirical findings developing at the interface between ecology and evolutionary biology. Eco-evolutionary models explore feedback loops between genes, organisms and the physical or biological components outside the organism's body. This changes our understanding of how organisms interact with their environment and the functional and evolutionary significance of biologically induced landforms. In the niche construction framework, genes can be conceived as the foundational evolutionary units of selection and inheritance, and everything beyond of this unit can be considered as the 'environment' for gene expression, either packaged within or unpackaged outside the organism. Both the packaged biological and unpackaged environments can be influenced by genes and manufactured by organisms, respectively, in the form of phenotypes or niche constructions. We propose that biomineralized structures, such as bones, osteoderms, antlers and shells, which can be packaged at varying degrees within an organism, as well as external products of genes such as termite mounds, which are unpackaged at the periphery of the organism, form a gradient of variation in the relative dominance and functional integration of biotic and abiotic components in ecosystems. A more explicit consideration of the functional interrelationships between physical and biological components transcending their traditional boundaries should promote a re-evaluation of the dichotomy between biological and geomorphological entities.

KEYWORDS
biogeomorphology, biomineralization, eco-evolutionary feedbacks, environment, natural selection, niche construction

## 1 | INTRODUCTION

The field of geomorphology aims to describe, analyse and understand Earth surface processes and landforms. It addresses a wide range of possible forms and patterns of mineral, rock, sediment and ice arrangements, spanning various spatiotemporal scales from microstructures detectable by electron microscopy, such as mechanical abrasion features on sand grains, to continental structures detectable by satellite, such as mountain ranges. In its traditional conception, geomorphology focuses on the fluxes of the mineral matter that constitutes the lithosphere and its interactions with endogenic forces and the atmosphere, the hydrosphere and the cryosphere. It is particularly concerned with the cycles of release, transfer and organization of mineral matter at the Earth's surface, with a dichotomy established between physical and biological compartments (Figure 1a).

Many minerals and geomorphological structures on the Earth's surface are modulated or directly constructed by organisms. In common usage, a mineral is defined as a non-organic matter that occurs naturally on Earth and is formed and transformed through geological and physicochemical processes (Nickel, 1995). However, organisms

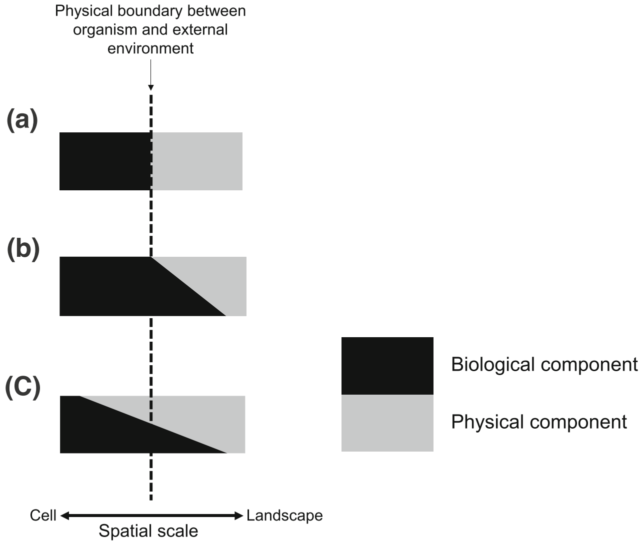

**FIGURE 1** Three different conceptual views of the relation between the biological and physical compartments. At a global scale, the biological compartment corresponds to the biosphere and the physical compartment to the hydrosphere, atmosphere and lithosphere; (a) standard conception in geomorphology with a clear dichotomy between the biological and physical compartments, though acknowledging some mutual influences; (b) biogeomorphological conception in which organisms affect the physical compartment and vice-versa, often with reciprocal interactions, and relatively few systems overwhelmingly dominated by physical or biological factors; (c) new conception integrating the biological and physical compartments, but with a continuum of potential dominance or relative importance. The linear variation in relative influence of biological versus physical influence and sharp separation between the two is a simplification of what is surely a more complex relationship.

have a profound and lasting effect on Earth's minerals (Knoll, 2003). Up to two-thirds of the approximately 5900 mineral species on Earth listed in the IMA Database of Mineral Properties (https://rruff.info/ima/; Morrison et al., 2017) have a direct or indirect biotic origin (Hazen, 2019; Hazen et al., 2008; Hystad et al., 2019). In addition to mineral formation, organisms also play an active role in sediment translocation and organization on Earth's surface through their activities. Recent research has demonstrated that the global rates of bioweathering and bioturbation are as rapid as the maximum rates of tectonic uplift in terms of mineral matter remobilization, highlighting the significant impact of biological processes on the Earth's surface (Phillips, 2009a; Wilkinson et al., 2009). The question of the role played by life in the physical compartment of ecosystems has thus become a significant new challenge in geomorphology (Figure 1b) (Phillips, 2016b, 2021).

Many unicellular and multicellular organisms consist of a significant fraction of mineral structures. However, the mineral structures that develop within or at the surface of organisms have never been considered from a biogeomorphological standpoint. A more explicit consideration of the functional interrelationships between physical and biological components in ecosystems, transcending their traditional boundaries, should promote a re-evaluation of the dichotomy between living and geomorphological entities.

We propose revisiting the basic premises of biogeomorphology with the proposition that the traditional dichotomy between living and non-living components (i.e., inside and outside) of biogeomorphological entities is convenient but may be too limiting. We suggest that the boundary between abiotic and biotic components and factors needs to be defined according to the questions being asked and the systems, entities and processes being studied. The idea presented in this article places rigid mineralized structures along gradients of packaging and functional integration with biological components from the cellular to the landscape levels (Figure 1c). This approach can broaden the conceptual and technical frameworks available to biogeomorphologists and evolutionary biologists for analysing feedbacks between organisms and the physical environment.

By reframing the way biogeomorphology conceptualizes 'inside' and 'outside', with reference to the distinction between the physical and biological environments, and by understanding why the problem of the abiotic-biotic boundary can be traced back to the formation of the first cells billions of years ago, we aim to disrupt the frameworks within which geomorphologists and biologists have long worked. Our proposed ideas are not meant to correct the standard views and syntheses of previous geomorphologists and biologists; rather, they are intended to link form and function in a biogeomorphological eco-evolutionary perspective that transcends the levels of organization of ecosystems.

Firstly, we introduce key concepts that stem from evolutionary biology and have influenced biogeomorphology. Next, we summarize the latest conceptual developments in the field of biogeomorphology and reconsider the boundaries between the internal and external aspects of organisms in light of the new biogeomorphological eco-evolutionary perspective. We also examine how mineralized structures on the Earth's surface can be classified based on a spectrum of biological packaging. Finally, we propose four examples of research perspectives at the interface between geomorphology and evolutionary biology.

## 2 | FOUNDATION CONCEPTS FROM EVOLUTIONARY BIOLOGY

The interdisciplinary field of biogeomorphology traces its origins to the naturalistic approaches of early pioneers of modern evolutionary biology and ecology. These precursors recognized the critical role of organisms in shaping their physical environment and the subsequent impacts of environmental feedbacks on evolution. Darwin (1881) observed that invertebrates can significantly influence soil and landscape dynamics through bioturbation and that these biotically modified environments can, in turn, affect natural selection through feedback loops (Johnson, 2002; Meysman et al., 2006). Similarly, Cowles (1899) conducted studies on the formation of sand dunes along the shores of Lake Michigan, USA, and proposed an integrative model of reciprocal coupling between dune formation and vegetation succession (Stallins, 2006). These early observations represent the first steps towards developing models of organisms actively modifying their physical environment, which subsequently affects their ecological and evolutionary trajectories.

In addition to the internal disciplinary advancements within biogeomorphology, as reviewed by Viles in (2011) and (2020), conceptual developments in ecology and evolutionary biology have served as catalysts for inspiring new research in the field. For example, Jones et al.

(1994) have contributed to this growing area of study by proposing the concept of ecosystem engineering. This concept, originating from the ideas of keystone and foundation species (Mills et al., 1993; Naiman et al., 1988; Paine, 1966), regards biogeomorphological interactions as a process in which organisms influence the structure and function of ecosystems by causing alterations in the physical environment. The explicit consideration of the geomorphological components of the habitat as key factors by the authors has clearly impacted biogeomorphology (Corenblit et al., 2011; Jones, 2012, Viles, 2020).

Advances in biogeomorphology have also been based on earlier evolutionary biology concepts such as Dawkins' (1982) extended phenotype (e.g., see Phillips, 2016a). The extended phenotype is a concept that highlights the wider effects of an organism's gene on its behaviour and artefacts. Although the phenotype typically refers to the observable and measurable traits of an organism resulting from the interaction between genetic and environmental factors, it is not restricted to just the organism's proteins and organic tissues or its physiology and behaviour. Instead, the extended phenotype encompasses all the effects that genes may have on external biological entities, such as other individuals of the same or different species, as well as the physical environment outside the organism's body, including minerals (see also Turner, 2004). The extended phenotype describes the underlying role of specific alleles of organisms in shaping their environment and the selective feedback to those same alleles. For example, this has been illustrated by the North American beavers *Castor canadensis* that build dams along rivers that drastically modify the flows of water, sediment and organic matter, creating ponds that, in turn, are used by the beavers specially to build their fortress huts. These changes in the physical environment are known to keep constant the selection pressures experienced by the beavers themselves but also other species in the ecosystem (Naiman et al., 1988; Wright et al., 2006). Hu and Hoekstra (2017) also illustrated the phenomenon by showing that burrowing behaviour of different fossorial deer mouse species (*Peromyscus* spp.) has evolved with variations in burrow morphology related to the selection of specific alleles (see also Weber et al., 2013; Weber & Hoekstra, 2009).

The more recent eco-evolutionary approach, which integrates ecological and evolutionary processes in a more explicit way, has attracted increasing interest and debate since the early 2000s (e.g., Bassar et al., 2021; Erwin, 2008; Hendry, 2017, 2019; Laland et al., 2016; Loreau, 2010; Matthews et al., 2011, 2014; Odling-Smee et al., 2003; Post & Palkovacs, 2009; Ware et al., 2019). Its underlying concept is based on the consideration that ecological and evolutionary changes can be congruent over short and long timescales and can generate stable and resilient emergent ecological structures and interaction networks (Fronhofer et al., 2023; Gibling & Davies, 2012; Govaert et al., 2019; Hendry, 2017; Matthews et al., 2014; Sultan, 2015). Eco-evolutionary models have helped establish reciprocal couplings between ecological processes, such as population growth, resource competition, trophic and other types of interaction networks and fluxes of matter and energy in modified landscapes, that occur at higher levels of ecosystems, and molecular structures and processes, such as DNA transcription to RNA, RNA translation into proteins, or gene mutation and expression, that occur at the lowest molecular level (Hendry, 2017). These models have highlighted the key role played by genetic variation (evolving both under genetic drift and natural selection) within a population at the community and ecosystem levels, as well as the role of higher levels of emerging ecological, physical, social and cultural phenomena on gene expression and selection in a feedback loop (Govaert et al., 2019; Jablonka & Lamb, 2005).

Although gene-centred models such as Dawkins' have been popular in evolutionary biology, alternative perspectives such as the triple helix (Lewontin, 1983, 2001) have also emerged and placed a greater emphasis on feedbacks between lower and higher levels of biological organization. The triple helix model considered the interplay between genes, organisms (or phenotypes) and the environment and highlighted the feedback loops that exist between these components. Lewontin's writings stimulated research into niche construction (sensu Odling-Smee et al., 2003; Sultan, 2015), which more explicitly refers to the process by which organisms modify their environment in ways that significantly affect their own fitness and that of other organisms present in the modified or constructed environment—a framework integrated in recent eco-evolutionary thinking (Hendry, 2017; Loreau, 2010).

This work also investigates feedbacks between organisms and their biotic or abiotic environment, which can drive evolutionary change and shape ecological dynamics. Niche construction is an example of a flexible model considering effects on other species and how ecological and evolutionary processes can be tightly intertwined. For instance, niche construction encompasses feedbacks from the constructed environment to other genes and ecological legacies arising from the niche construction of ancestors (known as ecological inheritance; Lehmann, 2008; Odling-Smee et al., 1996, 2003, 2013).

The authors are aware that evolutionary biologists are debating on the usefulness of the niche construction concept in the light of the modern and the extended evolutionary syntheses (e.g., Laland et al., 2014; Lewens, 2019). However, the present paper is not about this debate. Its aim is to show the usefulness of the niche construction concept for biogeomorphologists to better understand how organisms interact with their environment and thus contribute to the creation and modulation of biologically induced landforms. In this respect, the concept of niche construction contributed in blurring, to a certain extent, the boundaries between biological and geomorphological processes and led to the consideration that genetic variability within a population or a community may affect structures in the geomorphological environment and that, in turn, the modulated biotically controlled landforms may act as a selective force (e.g., Corenblit et al., 2010; Erwin, 2008; Phillips, 2008; Smith, 1986; Steiger & Corenblit, 2012).

## 3 | TOWARD A BIOGEOMORPHOLOGICAL ECO-EVOLUTIONARY PERSPECTIVE

The consideration in marine and terrestrial geology of the role of certain organisms in creating minerals and geological structures at continental scales such as massive limestone deposits and coral reefs has extended geological research to the indirect and direct role of organisms in shaping the Earth's surface over the long term (Benton & Xie, 2014) as well as, recently, in the dynamics of melting in Earth's mantle (Spencer et al., 2022). Since the publication of Viles' foundational volume in 1988, the field of biogeomorphology has made significant progress. This interdisciplinary field explores the intricate network of interactions between organisms and geomorphology (Naylor et al., 2002; Phillips, 2021). In addition to the effect of plants on landforms (Gurnell, 2014; Stallins, 2006), zoogeomorphology has included bacterial bioweathering on rocks, animal artefacts such as beaver dams, large animal and social insect mounds, galleries and nests as relevant objects in geomorphological studies (Bétard, 2021; Butler, 1995; Naylor et al., 2002; Viles, 2012; Viles et al., 2020).

A decade ago, the integration of insights from geomorphology and evolutionary biology gave rise to the sub-discipline of evolutionary geomorphology, as described by Steiger and Corenblit (2012). Compared with earlier, more general concepts of non-Darwinian evolutionary geomorphology (Huggett, 1995; Phillips, 2009b, 2006), this new sub-discipline considers the reciprocal couplings between organism evolution and Earth surface processes and landforms connected to biological activity (Corenblit et al., 2011, 2021; Kim & Lee, 2022; Phillips, 2016a, 2016b; Stallins & Corenblit, 2018). The field of biogeomorphology has since expanded with complementary conceptual models seeking to understand feedback loops between genes, organisms and geomorphological component of their environment, for example, the biogeomorphological life cycle (Corenblit et al., 2014), extended composite phenotypes (Phillips, 2016a) and the biogeomorphic feedback window (Eichel et al., 2016).

Although standard geomorphological and ecological approaches remain restricted to the examination of discrete tangible or abstract entities (e.g., respectively: sand grain, dune, alluvial bar or hydrographic network; DNA, RNA molecules, proteins, cell, organism, population, species and communities) and their interaction with their environment, the biogeomorphological eco-evolutionary perspective focuses on the chain of reciprocal causalities between landform and function into an ecological and evolutionary perspective (Corenblit et al., 2021; Fisher et al., 2007). The recent biogeomorphological models allow us to move beyond classical process-response system analyses in geomorphological systems (e.g., Phillips, 1995) and focus more on functional structures and mechanisms that link organism characteristics and geomorphological components. For instance, this involves not only looking at a beaver dam, pond and river channel but also examining the eco-evolutionary functional connections between the characteristics of beaver dams, ponds and river channels, as well as the phenotypes of beavers and the local community structure and function within the constructed environment (Larsen et al., 2021). In this conception, both the abiotic and biotic components of a biogeomorphological unit are viewed as functional elements nested in a feedback network at different levels, from molecules (especially nucleic acids and proteins) to communities, explicitly including geomorphological components of ecosystems (Corenblit et al., 2010, 2011; Fisher et al., 2007; Phillips, 2016a; Stallins, 2006; Stallins & Corenblit, 2018). Numerous examples of functional biogeomorphological units can be provided, such as fossorial animals (e.g., insects, worms, small and large mammals and reptiles) nests (Corenblit et al., 2021), termite mounds (Dangerfield et al., 1998) and vegetated foredunes (Stallins & Corenblit, 2018).

However, understandings in biogeomorphology were primarily developed based on the following premises: (i) organisms and their assemblages, such as populations, groups, societies and communities, are the operational levels of biological integration for reasoning and analysing the feedback between life and geomorphology. (ii) The organism level provides the physical boundary between the biological and geomorphological compartments. Biogeomorphological structures are thought to develop outside of organisms, that is, in their external environment, and therefore, the organism represents the reference unit for physical distinction between the internal biological compartment and the external physical compartment (Figure 1a). (iii) Thus, a rational dichotomy exists between the living and non-living components in ecosystems.

## 4 | REVISITING INTERNAL-EXTERNAL BOUNDARIES OF ORGANISMS

The original Darwinian selection acted about four billion years ago on molecular self-replication, probably in a primordial prebiotic liquid environment in the ocean or in hot springs (Damer & Deamer, 2020; Gargaud et al., 2011; Hazen & Sverjensky, 2010; Martin et al., 2008; Sojo et al., 2016). The sorting of genetic elements in the prebiotic environment led to the proliferation and selection of increasingly complex molecular structures with replication advantages. Compartmentalization was a key step in the early evolution of life (Daemer et al., 2002; Szathmáry & Maynard Smith, 1995). The origin of cell membranes remains an unresolved issue (Deamer, 2017; Koga et al., 1998; Lombard et al., 2012; Martin & Russell, 2003; Wächtershäuser, 2003). The evolution of the cell membrane through biosynthesis defined at least 3.5 Ga a boundary between what has permanently become (through trillions of trillions of generations of cell division) the internal cellular environment of the genes constituted of the cytosol and the organelles and their external environment in which they were originally formed (Gill & Forterre, 2016; Koonin & Martin, 2005; Lombard et al., 2012).

The cell is considered as the most fundamental living entity with its ability to reproduce, use energy, grow and develop, keep homeostasis, respond to stimuli from the environment and adapt through evolution (Szathmáry, 2015; Szathmáry & Maynard Smith, 1995). Viruses are not considered here because, even if they are ecologically and evolutionarily intertwined with their cellular hosts and play a significant role in evolution (Harris & Hill, 2021), they are not independently self-replicating and are usually not thought of as living entities (Moreira & López-García, 2009). Life forms evolved from the first single-cell organisms to cell colonies, multicellular organisms and, finally, to societies of organisms (superorganisms, e.g., insect societies). The major evolutionary transitions (Szathmáry, 2015; Szathmáry & Maynard Smith, 1995; West et al., 2015) for living entities were characterized by the emergence of (i) the individual entities (archaea, eubacteria and eukaryotic cells); (ii) the specialization of eukaryotic cells to form different tissues, organs and organ systems defining the multicellular organismal entity; and (iii) finally, to the specialization of individual organisms to form a society. The evolution of multicellularity and societies (notably insect ones) represented important steps in evolution that resulted in an increased complexity of feedbacks between life and the physical environment, including geomorphological components at various spatial scales and organizational levels.

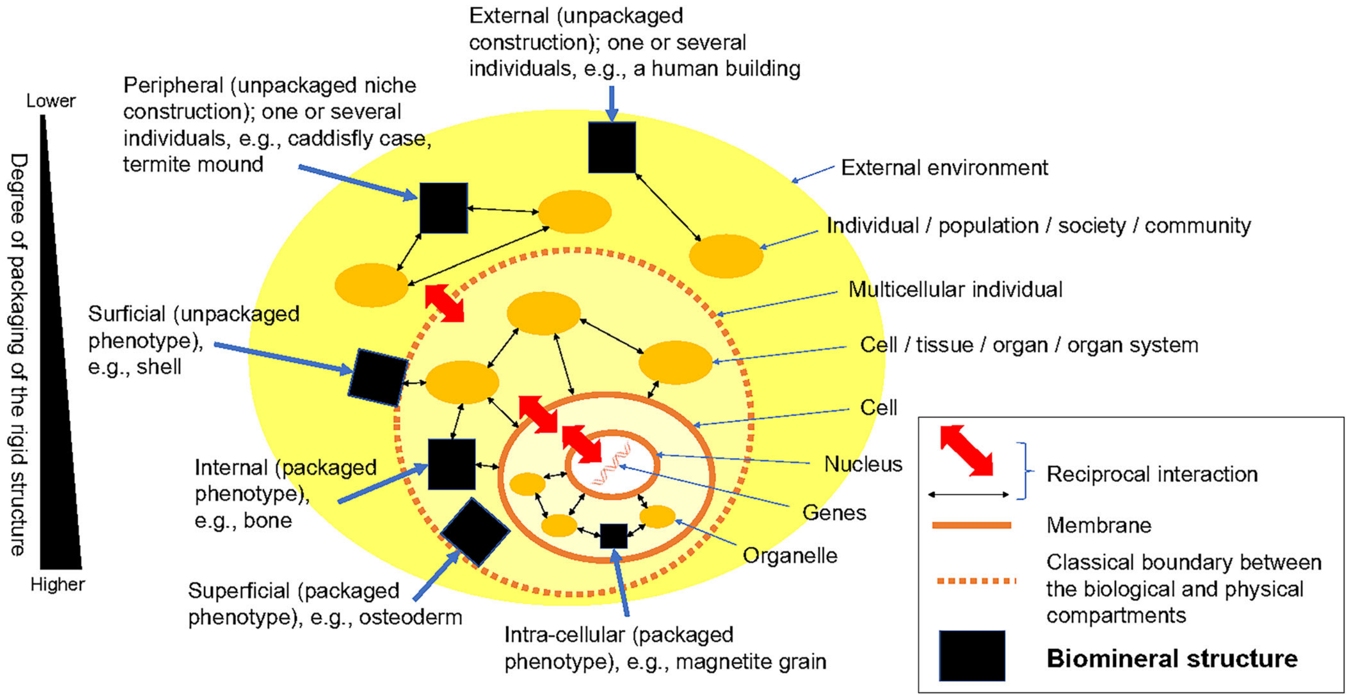

**FIGURE 2** Conceptual framework connecting the different environments of the genes in a nested hierarchy of reciprocal interactions. Each environmental level encompasses biological and physical (mineral) components constituting a network of feedbacks. On Earth, the limits of the external environment correspond to the ionosphere and the deep lithosphere. [Color figure can be viewed at wileyonlinelibrary.com]

The formation of the first cells is a primordial phenotype construction and the subsequent phenotype construction, that is, the formation of internal organelles such as mitochondria and chloroplasts as a consequence of endosymbiosis, and the following major evolutionary transitions were iterative exaptations of that event. In this line, phenotype construction is both a developmental process and a driver of evolution (Laland et al., 2008; Odling-Smee et al., 2003). The genes that control body development are themselves selected in response to changes in the selective environment that result from hierarchical reciprocity between lower and upper levels of biological organization (Laland & Sterelny, 2006; Love, 2006).

This corresponds to eco-evo-devo dynamics, which refer to the interplay of ecological factors influencing evolutionary processes and, in turn, developmental processes contributing to the diversification and adaptation of species (Gilbert & Epel, 2009; Pfennig et al., 2010; West-Eberhard, 2003). Because of these dynamics, new environmental conditions are created, both internally (in the form of phenotypes) and externally (as niche constructions), allowing for subsequent phases of development to occur in response to changing environmental conditions (Gilbert et al., 2015). Phenotypic plasticity plays a crucial role in providing a direct mechanism through which organisms adjust trait variation in response to environmental changes (Ghalambor et al., 2007; Gilbert, 2001). As a result, organisms undergo their development phases in a tightly coupled, reciprocal relationship with their environment, with the ontogenetic environment acting as both a cause and an effect of the organism's development (Amundson, 2005; Laland et al., 2008; Lewontin, 1983; Müller, 2007). As suggested by Torday (2016) and Torday and Miller (2016), the phenotype can be considered an 'internal niche construction', rather than the traditional reasoning of Odling-Smee et al. (2003) in which niche construction is considered as organisms shaping their external environment. In such a perspective, the development and phenotypic variation of an organism phenotype, its evolutionary history and its ecological interactions are interconnected and mutually influential.

Following that line, we can consider that genes are found in ecosystems in nested compartments, each corresponding to a possible level of gene expression and selection as organic, physical or even immaterial (behaviour) phenotypes (Laland et al., 1999). Beyond the gene—which is defined as the most fundamental replicator unit and, therefore, unit of selection—everything comes down to internal and external environments with varying degrees of biotic influence, as well as the packaging and integration of biological (organic) and physical (mineral) structures (Figure 2).

## 5 | REPLACING MINERAL STRUCTURES INTO A GRADIENT OF BIOLOGICAL PACKAGING

Abiotic and biotic components of the Earth are mixed everywhere from the Earth's crust (Bose et al., 2020) to the atmosphere (Delort et al., 2010), and nothing in this envelope can be considered as completely abiotic in terms of the complete absence of life or its direct or indirect influence. Even geophysical fluid dynamics, which can certainly be undertaken without direct consideration of biotic influences, operate in environments whose properties are largely determined by the presence of the biosphere. Thus, on a continuum that extends to the absolute abiotic, one would have to go all the way down to the mantle or up to the ionosphere. Conversely, how far down in the biological compartment do we need to go to be totally, absolutely biotic, as even biological entities are constituted of an important fraction of the major components of the physical realm?

Unicellular and multicellular organisms take up mineral elements (e.g., Ca, Si and P) in their external environment and typically generate rigid structures constituted mainly of $CaPO_4$, $CaCO_3$ or $SiO_2$, most often for the purpose of hardening or stiffening their tissues (Knoll, 2003), for example, bones, osteoderms, teeth, antlers, eggs and shells (Mann, 2001; Murdock & Donoghue, 2011). Intracellular biomineralization widely occurs in cells (Lin et al., 2014), but here for simplicity, we consider only extracellular biomineral structures. Diatoms, a type of unicellular algae that are photosynthetic protists and that are abundant in various aquatic ecosystems, are recognized for their intricate cell walls made of silica, known as a frustule (De Tommasi et al., 2017). Biominerals include various types of materials such as iron and gold in single-celled organisms, silicates or carbonates in diatoms and calcium carbonates and phosphates in vertebrates (Boskey, 2003).

These structures are organism-regulated and typically complex in material, size and shape and are created for various functions such as maintenance, protection, movement, feeding, sexual attraction, communication and also storing ions. The physiological means by which organisms precipitate minerals and the forms and functions of the biomineralized structures they create are the result of evolution (Knoll, 2003). The biomineralization process thus maintains a functional coupling between the inert (mineral) and the living (organic) components of the Earth, and biomineralization thus demarcates from organomineralization that refers to more indirect contributions of life to mineralization (Perry et al., 2007).

Biomineralization is a widespread and very ancestral process that appeared in different clades several times over the evolutionary time scale (Murdock & Donoghue, 2011; Pérez-Huerta et al., 2018). In most cases, they are mineral–organic hybrids; minerals constitute the dominant fraction, and organic compounds are a minority or ultra-minority (LeGeros, 1981). In animals, the silica biomineral (opaline silica) is restricted to siliceous sponges, but calcareous (calcite or aragonite) and phosphatic (calcium phosphate) biominerals are present in all major divisions across the major phyla levels of the animal tree, that is, vertebrates, echinoderms, molluscs and sponges (Murdock, 2020; Murdock & Donoghue, 2011).

Carbonate minerals are an important component of the Earth's sedimentary geologic record. The textural and structural properties and chemical composition of marine carbonate sediments are proxies used to access the deep history of geological processes, carbon and oxygen cycles and biological evolution (Schidlowski, 1988). Marine carbonate sediments have therefore been widely studied in geology, geochemistry and palaeontology (Ahm et al., 2018; Blättler & Higgins, 2017; Higgins et al., 2018; for a review, see Reijmer, 2021). The uptake of minerals by organisms from the external physical environment, their nucleation and organization within or at the surface of organisms and their release into the external environment form a global carbonate mineral cycle in which life plays a central role (Figure 3). The biogeomorphological cycle of carbonate minerals (BCCM hereafter) has profoundly affected the geomorphology and geochemistry of the Earth's surface in ways that uniquely distinguish it from other telluric planets. On a global scale, the massive uptake of dissolved mineral elements by organisms from the physical compartment is followed by massive storage and organization of these minerals in the biological compartment (i.e., within organisms), which contributes to the development and functioning of organisms. At this stage of the cycle, mineral forms are associated with biological functions and are shaped by stochastic and deterministic evolutionary processes. Most of the calcite and aragonite on Earth are a product of calcifying organisms (Zeebe & Westbroek, 2003). When organisms die, many of the biomineralized structures they created when alive

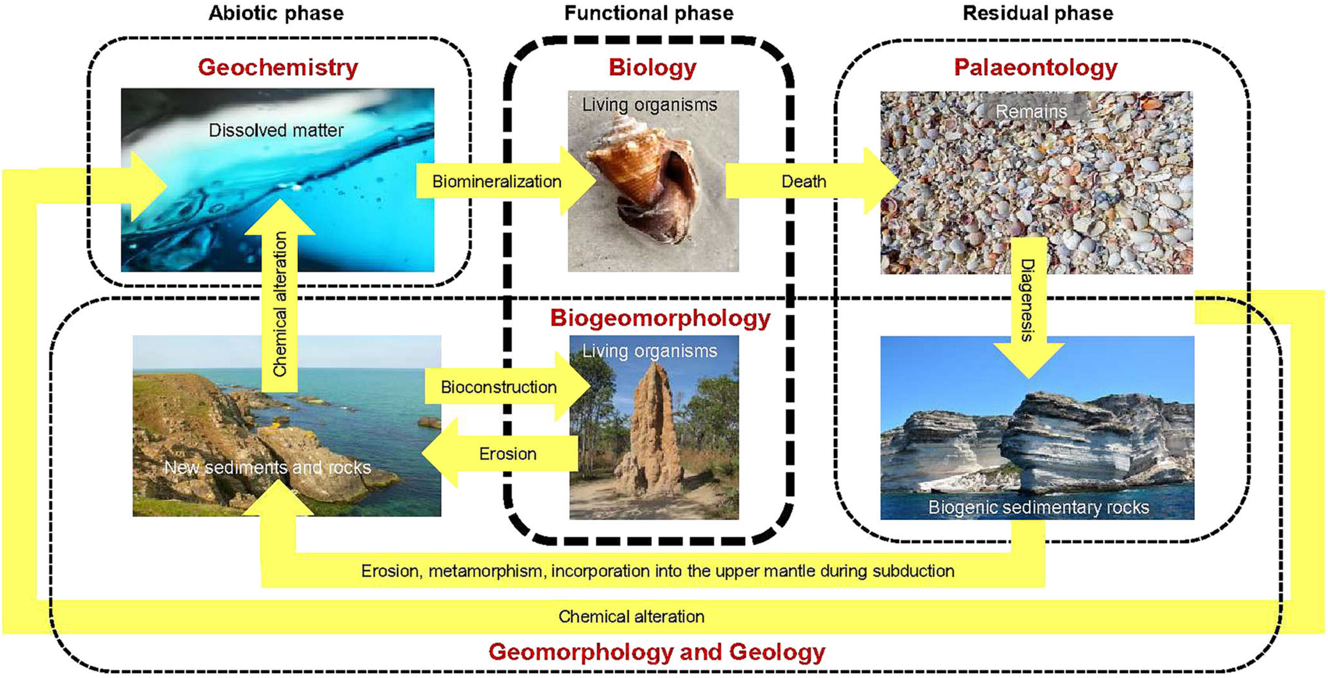

FIGURE 3 Biogeomorphological cycle of carbonate minerals (BCCM). The scientific disciplines interested in studying the different phases are indicated in red. Photos are under Creative Commons license; from top left to bottom right: fox_kiyo; Alex Bellink; cquintin; WalkInfo, brewbooks; paularps. [Color figure can be viewed at wileyonlinelibrary.com]

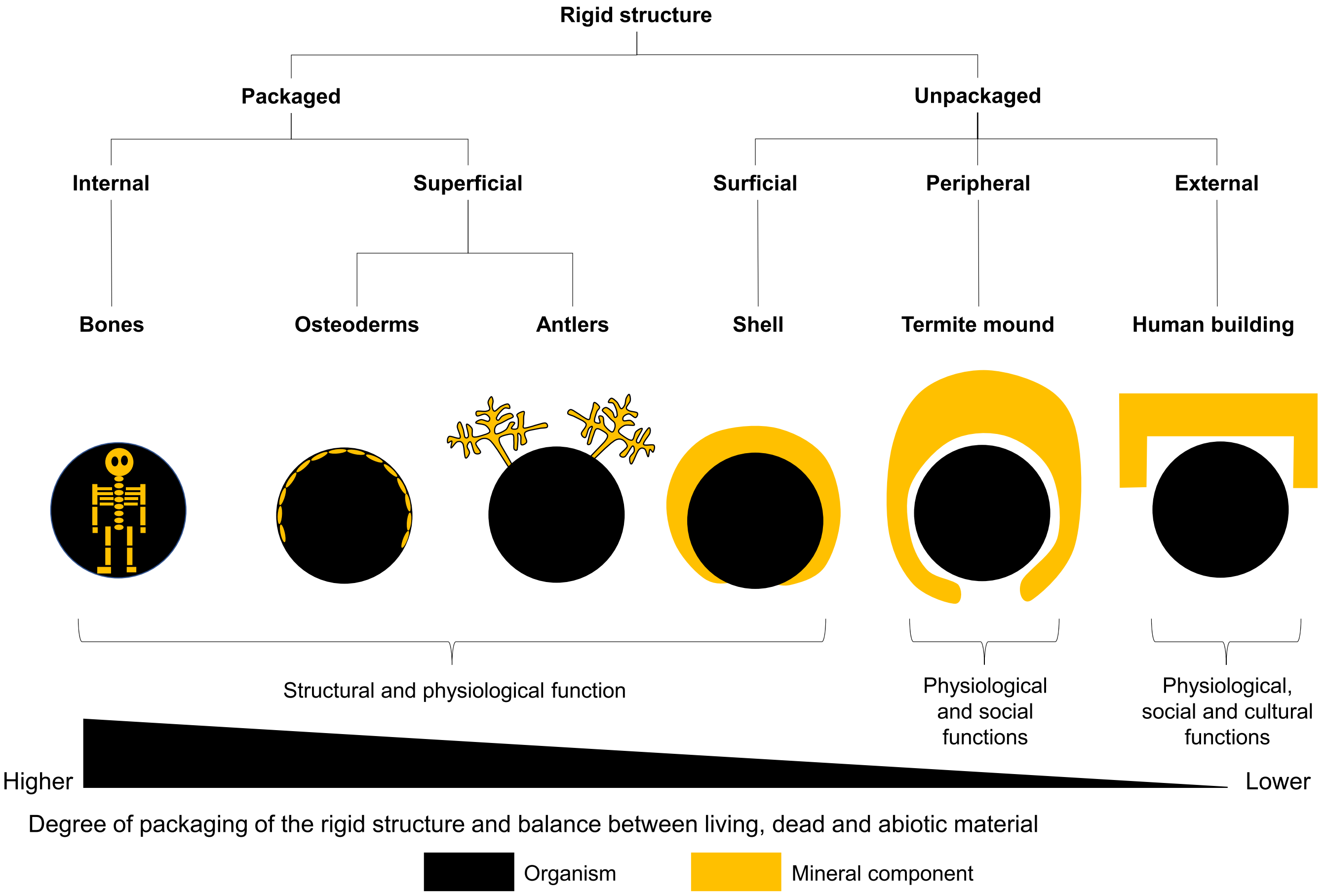

**FIGURE 4** Conceptual model showing a simplified continuum of (i) degree of packaging of biotically induced rigid structures; (ii) balance between living, dead and abiotic material and (iii) degree in which it is genetically controlled. [Color figure can be viewed at wileyonlinelibrary.com]

are retained much longer than the organisms' soft tissue (Phillips, 2016b). Carbonate minerals are deposited in both shallow and deep oceans, and abandoned biomineralized structures can accumulate over millions of years on oceanic platforms, forming extensive and ancient geomorphological structures (Milliman, 1993). These structures contribute to the formation of vast plateaus and mountain ranges resulting from tectonic uplift, such as the Himalayas. Diagenesis and tectonics led to the formation of limestone, marble and dolomite in these zones, which currently cover approximately 20% of the terrestrial surface (Martin, 2017). Carbonate minerals are soluble, and their dissolution contributes to approximately 50% of the global loads of calcium and magnesium in rivers (Meybeck, 1987).

From a geomorphological perspective, the BCCM comprises three distinct phases, each contributing to Earth surface landforms. The first phase is characterized by native structures adjusting to physical and chemical constraints (abiotic phase in Figure 3). The second phase includes functional components built by organisms that result from evolution and interactions between biotic and abiotic elements of ecosystems (functional phase). The final phase is composed of 'dead' remnants that accumulate in geologic reservoirs, which can be affected by tectonic forces and are progressively altered mechanically, thermally and/or chemically (residual phase) (Corenblit et al., 2010).

Rigid mineral structures that are built by organisms and that are to various degrees (e.g., bones, osteoderms, antlers and shells), or not at all (e.g., caddisfly cases, termite mounds and bird nests) incorporated within the internal environment of the organism may have different connections with the organic matter. The degree of hybridization between living organic matter (i.e., living cells), non-living organic compounds (proteins) and mineral matter is related to the degree of incorporation of a rigid structure. Bones are considered hard 'living tissue' because they contain a small fraction of living cells (i.e., osteoblasts, osteoclasts and osteocytes) and can regenerate. In contrast, mollusc shells can be regenerated by the adhering living tissues but are considered 'dead tissue' because they consist of a mixture of mineral matter and proteins without the inclusion of living cells. Some external termite mounds or bird nests are made of a mixture of mineral material and organic secretions (Ocko et al., 2019), whereas other nests are made solely of biologically agglomerated mineral material (Figure 4). Vertebrates and molluscs have a skeleton or shell that represents a structural component physically inseparable from living matter. In contrast, a termite mound (and furthermore an ant nest) represents a functionally but not physically inseparable component because termites can temporarily leave the mound. However, unlike ants, most of the termite species are typically constrained to build and use foraging galleries and never forage outside, the galleries being an extension of the mound (kind of frozen pseudopods). Human-built structures and people are structurally and functionally dissociable because humans can leave the mineral building and survive outside of it (although often only through reliance on other constructions, such as clothes, fire and technology).

## 6 | PERSPECTIVES

The discipline of geomorphology should consider more components and processes than just the physical breakdown of materials and their erosion, transport and deposition by physical agents (Phillips, 2021). Although the compartmentalization of disciplines to study the biogeomorphological cycle is practical, the BCCM itself represents a continuum of matter and energy transformation, which should also be considered as a unique macroscopic structure with interdisciplinary interpretations (Figure 3). The conceptual proposal of this paper is not to suggest that biogeomorphologists become surrogates for biologists and anatomists but rather to encourage them to work closely with these fields to expand their discipline's horizons and establish links between form and biological function along a biogeomorphological gradient of reciprocal coupling between physical and biological components, as already proposed in biogeomorphology (Corenblit et al., 2011; Fisher et al., 2007; Stallins, 2006).

This paper proposes an approach that transcends standard boundaries between abiotic and biotic compartments and adopts a more inclusive and functional way of examining how geomorphological structures on Earth's surface are embedded in a cycle of mineral matter transformation. By examining notions such as 'organism', 'living entity', 'unit of selection', 'environment', 'internality, 'externality' and 'matter and energy cycle' from a different conceptual perspective, we can enhance our understanding of the relationship between life and geomorphological structures. The perspective is timely, given the current excitement surrounding eco-evolutionary questions (Fronhofer et al., 2023; Hendry, 2017; Loreau, 2010). This could lead to new opportunities for collaboration between geomorphologists and evolutionary biologists, potentially resulting in improved biogeomorphological models.

In this approach, geomorphological components are seen as both a product of organisms and, in turn, essential to organisms' functioning, development and evolution. The eco-evolutionary approach also examines how traits develop in response to environmental cues, potentially biotically controlled in the case of niche construction, and how this development influences the evolution of organisms over time. This expanded approach considers not only the role of environmental factors and genetic variation in controlling trait variation but also the dynamic interplay between physical and biological components in shaping geomorphological structures.

In the light of the here presented introspective perspective, new questions at the interface between evolutionary biology and geomorphology need to be asked and tested. Four points are proposed:

i. Recent developments have pointed out the role of symbiosis and cooperation in biological organization. It contributed to blurring the boundaries between individual entities and offered new perspectives to characterize the 'biological individual' (Gilbert et al., 2012). It was suggested that anatomical and physiological criteria are not relevant for defining an animal or a plant as an individual because it is constituted of a diversity of symbionts carrying fundamental metabolic, physiological and developmental functions. The holobiont theory suggests that a host and its symbiotic microbes are to be considered as a single entity in the evolutionary perspective (Gilbert et al., 2012; Stencel & Wloch-Salamon, 2018). In that sense, the hologenome theory of evolution (Zilber-Rosenberg & Rosenberg, 2008) stated that from an evolutionary perspective, a host is inseparable from its associated microbiome. Together, the host and the microbiome (i.e., the holobiont) may form a coherent unit of selection, and thus, the genomes of the host and the microbiome (i.e., the hologenome) form a genetic unit for its evolution. These integrative perspectives open new avenues for conceptually and practically redefining living entities as ecosystems (see Szathmáry & Maynard Smith, 1995) subjected to and affecting genes, potentially with the inclusion of packaged or unpackaged physical structures. For example, coral colony polyps build extensive bioconstructions in the oceans, that is, coral reefs (Tambutté et al., 2011). Such large-scale biogeomorphological structures covering about 284,300 km$^2$ (Spalding et al., 2001) result from genetic reciprocal interactions between hosts and their symbionts and also feedbacks with the biomineralized geomorphological structures they produce (Brambilla et al., 2021). Coral morphology affects water, sediment and nutrient flows and water temperature in a way that favours the polyp colony and other species (Brambilla et al., 2021; Monismith, 2007). Certain biomineral landforms are thus a functional product of co-evolution and cooperation between symbiotic or cooperating species. The structure forms a system driven by top-down and bottom-up eco-evolutionary feedbacks. New collaborations between biogeomorphologists and evolutionary biologists should be created for exploring the hypothesis that biogeomorphological units such as a coral reef represent a unit of selection.

ii. Internal, superficial and surficial structures (see Figure 4) that are restricted to the size and shape of the organism should adjust and evolve in accordance with the physiological and biomechanical constraints imposed by the body itself (internal constraints) and its relation with external physical constraints (e.g., gravity and water flow) over the successive generations of the individuals, whereas peripheral structures developing at larger spatial scales, and possibly across many generations, should provide extended physiological and biomechanical solutions and plasticity for the organisms to provide new adaptations at larger spatio-temporal scales to the external constraints and their fluctuations (Jones, 2012; Lehmann, 2008; Turner, 2000). The characteristics of rigid structures (e.g., size, shape, density, mass and plasticity) should be analysed from a biogeomorphological perspective according to the variation in the type of selection pressure that acts on them. It may be possible to propose formal biogeomorphological models that link parameters related to the mineralized structures to the ones describing the organisms that have produced the structure, for example, the total weight of the biomineralized structure (as a response variable) to the total weight of the cells that have produced the structure. The coefficients of the models may possibly vary according to (i) the degree of packaging (inside the body, superficial, surficial and peripheral) of the biomineralized structure and to (ii) the type of environment in which the organisms live (air, water, at ground surface or underground).

iii. The potential inclusion in biogeomorphology of the non-mineral rigid 'dead' tissues of animals (such as keratin and chitin) and also of plants (such as cellulose and lignin). Whether these non-mineral materials should be considered in biogeomorphology remains an interesting question, particularly with respect to plants. A large body of publications has illustrated the effects of plants on Earth surface processes and landforms in active geomorphological environments such as rivers, mangroves, coastal dune barriers and mountain hillslopes (Eichel et al., 2016; Gurnell, 2014; Stallins, 2006). Plants are able to affect geomorphological processes and landforms because they produce rigid and semi-rigid dead tissue capable of withstanding mechanical stress related to gravity, wind and water flow (Niklas, 1997; Vogel, 2020). We suggest that the relationship between wood production and characteristics and landform dynamics should be studied in a more integrative manner by considering dead plant tissues in living plants as a functional interface between the living part of the plant and the external environment with its mechanical constraints that also affect sediment and landform dynamics.

iv. The consideration of the stratigraphic records of fossilized rigid structures in collaboration with palaeontologists for a better understanding of the evolution of packaged internal, superficial and unpackaged surficial and peripheral rigid structures and their resulting effects on the global cycle and evolution of biogenic minerals. Such an approach may also contribute to developments in astrobiology. The different telluric planets of the solar system have reached different stages of mineral evolution (Hazen et al., 2008). The small planets without liquid water such as Mercury have low mineral diversity, whereas the mid-sized Mars could reach higher diversity of minerals. Bigger telluric planets such as Venus and the Earth produced granitoids. However, life mineral structures made the Earth a very particular case. Thus, minerals that are produced by organisms and their chemical and morphological signatures as known on the Earth may be used by analogy for identifying potential chemical, isotopic, textural and morphological signatures of life on other planets such as Mars (Corenblit et al., 2019; Lovelock, 1979).

Finally, based on the ideas presented here, we suggest that the discipline of biogeomorphology should again redefine its conceptual and practical boundaries and its connections with biological sciences and especially with the theory of evolution (Figure 3). This biogeomorphological introspection could lead to conceptual changes within the discipline of biogeomorphology with the replacement of the dichotomic view of biota and abiota by a bi-directional functional view of the reciprocal coupling between the biological and geomorphological compartments at various spatiotemporal scales along the continuum of mineral uptake in the physical environment, storage, organization and use in organisms and finally release and accumulation in the physical environment.

## AUTHOR CONTRIBUTIONS

Dov Corenblit, Bruno Corbara, Kevin Lala, Jonathan D. Phillips, Arnaud Pocheville, Erwan Roussel, Johannes Steiger and Heather A. Viles wrote the paper, have made substantial contributions to the conceptual conception and have been involved in drafting the manuscript and revising it critically. All authors read and approved the final manuscript.

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## CONFLICT OF INTEREST STATEMENT

No conflict of interest.

## DATA AVAILABILITY STATEMENT

No data were used in this conceptual article.

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## REFERENCES

Abouheif, E., Favé, M.J., Ibarrarán-Viniegra, A.S., Lesoway, M.P., Rafiqi, A.M. & Rajakumar, R. (2014) Eco-evo-devo: the time has come. *Ecological Genomics: Ecology and the Evolution of Genes and Genomes*, 781, 107–125. Available from: https://doi.org/10.1007/978-94-007-7347-9_6

Ahm, A.S., Bjerrum, C.J., Blättler, C.L., Swart, P.K. & Higgins, J.A. (2018) Quantifying early marine diagenesis in shallow-water carbonate sediments. *Geochimica et Cosmochimica Acta*, 236, 140–159. Available from: https://doi.org/10.1016/j.gca.2018.02.042

Amundson, R. (2005) *The changing role of the embryo in evolutionary thought*. Cambridge, UK: Cambridge University Press.

Bassar, R.D., Coulson, T., Travis, J. & Reznick, D.N. (2021) Towards a more precise–and accurate–view of eco-evolution. *Ecology Letters*, 24(4), 623–625. Available from: https://doi.org/10.1111/ele.13712

Benton, M.J. & Xie, S. (2014) Defining the discipline of geobiology. *National Science Review*, 1(4), 483–485. Available from: https://doi.org/10.1093/nsr/nwu052

Bertalanffy, F.D. & Lau, C. (1962) Cell renewal. *International Review of Cytology*, 13, 357–366. Available from: https://doi.org/10.1016/S0074-7696(08)60287-9

Bétard, F. (2021) Insects as zoogeomorphic agents: an extended review. *Earth Surface Processes and Landforms*, 46(1), 89–109. Available from: https://doi.org/10.1002/esp.4944

Blättler, C.L. & Higgins, J.A. (2017) Testing Urey's carbonate–silicate cycle using the calcium isotopic composition of sedimentary carbonates. *Earth and Planetary Science Letters*, 479, 241–251. Available from: https://doi.org/10.1016/j.epsl.2017.09.033

Bose, H., Dutta, A., Roy, A., Gupta, A., Mukhopadhyay, S., Mohapatra, B., et al. (2020) Microbial diversity of drilling fluids from 3000 m deep Koyna pilot borehole provides insights into the deep biosphere of continental earth crust. *Scientific Drilling*, 27, 1–23. Available from: https://doi.org/10.5194/sd-27-1-2020

Boskey, A.L. (2003) Biomineralization: an overview. *Connective Tissue Research*, 44(1), 5–9. Available from: https://doi.org/10.1080/03008200390152007

Brachert, T.C. & Dullo, W.C. (2000) Shallow burial diagenesis of skeletal carbonates: selective loss of aragonite shell material (Miocene to Recent, Queensland Plateau and Queensland Trough, NE Australia)—implications for shallow cool-water carbonates. *Sedimentary Geology*, 136(3–4), 169–187. Available from: https://doi.org/10.1016/S0037-0738(00)00096-8

Brambilla, V., Baird, A., Barbosa, M., Dehnert, I., Madin, J.S., Peddie, C., et al. (2021) Coral niche construction: coral recruitment increases along a coral-built structural complexity gradient. *bioRxiv*, Available from: https://doi.org/10.1101/2021.10.14.464352

Butler, D.R. (1995) *Zoogeomorphology: animals as geomorphologic agents*. Cambridge, UK: Cambridge University Press.

Corenblit, D., Baas, A.C.W., Bornette, G., Darrozes, J., Delmotte, S., Francis, R.A., et al. (2011) Feedbacks between geomorphology and biota controlling earth surface processes and landforms: a review of foundation concepts and current understandings. *Earth-Science Reviews* 106: 307–331. Available from: https://doi.org/10.1016/j.earscirev.2011.03.002

Corenblit, D., Corbara, B. & Steiger, J. (2021) Biogeomorphic eco-evolutionary feedback between life and geomorphology: a theoretical framework using fossorial mammals. *The Science of Nature*, 108(6), 1–16. Available from: https://doi.org/10.1007/s00114-021-01760-y

Corenblit, D., Darrozes, J., Julien, F., Otto, T., Roussel, E., Steiger, J., et al. (2019) The search for a signature of life on Mars: a biogeomorphological approach. *Astrobiology*, 19(10), 1279–1291. Available from: https://doi.org/10.1089/ast.2018.1969

Corenblit, D., Steiger, J. & Delmotte, S. (2010) Abiotic, residual and functional components of landforms. *Earth Surface Processes and Landforms*, 35(14), 1744–1750. Available from: https://doi.org/10.1002/esp.2064

Corenblit, D., Steiger, J., González, E., Gurnell, A.M., Charrier, G., Darrozes, J., et al. (2014) The biogeomorphological life cycle of poplars during the fluvial biogeomorphological succession: a special focus on *Populus nigra* L. *Earth Surface Processes and Landforms*, 39(4), 546–563. Available from: https://doi.org/10.1002/esp.3515

Corenblit, D., Tabacchi, E., Steiger, J. & Gurnell, A.M. (2007) Reciprocal interactions and adjustments between fluvial landforms and vegetation dynamics in river corridors: a review of complementary approaches. *Earth-Science Reviews*, 84(1-2), 56–86. Available from: https://doi.org/10.1016/j.earscirev.2007.05.004

Cowles, H.C. (1899) The ecological relations of vegetation on the sand dunes of Lake Michigan. *Botanical Gazette*, 27(2), 95–117. Available from: https://doi.org/10.1086/327796

Damer, B. & Deamer, D.W. (2020) The hot spring hypothesis for an origin of life. *Astrobiology*, 20(4), 429–452. Available from: https://doi.org/10.1089/ast.2019.2045

Dangerfield, J.M., McCarthy, T.S. & Ellery, W.N. (1998) The mound-building termite *Macrotermes michaelseni* as an ecosystem engineer. *Journal of Tropical Ecology*, 14(4), 507–520. Available from: https://doi.org/10.1017/S0266467498000364

Darwin, C. (1881) *The formation of vegetated mould through the action of worms with observation of their habitats*. London, UK: Murray.

Dawkins, R. (1976) *The selfish gene*. New York, USA: Oxford University Press.

Dawkins, R. (1982) *The extended phenotype*. Oxford, UK: Freeman.

De Tommasi, E., Gielis, J. & Rogato, A. (2017) Diatom frustule morphogenesis and function: a multidisciplinary survey. *Marine Genomics*, 35, 1–18. Available from: https://doi.org/10.1016/j.margen.2017.07.001

Deamer, D. (2017) The role of lipid membranes in life's origin. *Lifestyles*, 7(1), 5. Available from: https://doi.org/10.3390/life7010005

Deamer, D., Dworkin, J.P., Sandford, S.A., Bernstein, M.P. & Allamandola, L.J. (2002) The first cell membranes. *Astrobiology*, 2(4), 371–381. Available from: https://doi.org/10.1089/153110702762470482

Delort, A.M., Vaïtilingom, M., Amato, P., Sancelme, M., Parazols, M., Mailhot, G., et al. (2010) A short overview of the microbial population in clouds: potential roles in atmospheric chemistry and nucleation processes. *Atmospheric Research*, 98(2-4), 249–260. Available from: https://doi.org/10.1016/J.ATMOSRES.2010.07.004

Eichel, J., Corenblit, D. & Dikau, R. (2016) Conditions for feedbacks between geomorphic and vegetation dynamics on lateral moraine slopes: a biogeomorphic feedback window. *Earth Surface Processes and Landforms*, 41(3), 406–419. Available from: https://doi.org/10.1002/esp.3859

Erwin, D.H. (2008) Macroevolution of ecosystem engineering, niche construction and diversity. *Trends in Ecology & Evolution*, 23(6), 304–310. Available from: https://doi.org/10.1016/j.tree.2008.01.013

Fisher, S.G., Heffernan, J.B., Sponseller, R.A. & Welter, J.R. (2007) Functional ecomorphology: feedbacks between form and function in fluvial landscape ecosystems. *Geomorphology*, 89(1-2), 84–96. Available from: https://doi.org/10.1016/j.geomorph.2006.07.013

Fronhofer, E.A., Corenblit, D., Deshpande, J.N., Govaert, L., Huneman, P., Viard, F., et al. (2023) Eco-evolution from deep time to contemporary dynamics: the role of timescales and rate modulators. *Ecology Letters*, 26(Suppl. 1), S91–S108. Available from: https://doi.org/10.1111/ele.14222

Gargaud, M., López-Garcìa, P. & Martin, H. (Eds). (2011) *Origins and evolution of life: an astrobiological perspective*, Vol. 6. Cambridge University Press.

Ghalambor, C.K., McKay, J.K., Carroll, S.P. & Reznick, D.N. (2007) Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. *Functional Ecology*, 21(3), 394–407. Available from: https://doi.org/10.1111/j.1365-2435.2007.01283.x

Gibling, M.R. & Davies, N.S. (2012) Palaeozoic landscapes shaped by plant evolution. *Nature Geoscience*, 5(2), 99–105. Available from: https://doi.org/10.1038/ngeo1376

Gilbert, S.F. (2001) Ecological developmental biology: developmental biology meets the real world. *Developmental Biology*, 233(1), 1–12. Available from: https://doi.org/10.1006/dbio.2001.021

Gilbert, S.F., Bosch, T.C. & Ledón-Rettig, C. (2015) Eco-evo-devo: developmental symbiosis and developmental plasticity as evolutionary agents. *Nature Reviews Genetics*, 16(10), 611–622. Available from: https://doi.org/10.1038/nrg3982

Gilbert, S.F. & Epel, D. (2009) *Ecological developmental biology: integrating epigenetics, medicine, and evolution*. Sinauer Associates.

Gilbert, S.F., Sapp, J. & Tauber, A.I. (2012) A symbiotic view of life: we have never been individuals. *The Quarterly Review of Biology*, 87(4), 325–341. Available from: https://doi.org/10.1086/668166

Gill, S. & Forterre, P. (2016) Origin of life: LUCA and extracellular membrane vesicles (EMVs). *International Journal of Astrobiology*, 15(1), 7–15. Available from: https://doi.org/10.1017/S1473550415000282

Govaert, L., Fronhofer, E.A., Lion, S., Eizaguirre, C., Bonte, D., Egas, M., et al. (2019) Eco-evolutionary feedbacks-theoretical models and perspectives. *Functional Ecology*, 33(1), 13–30. Available from: https://doi.org/10.1111/1365-2435.13241

Gurnell, A. (2014) Plants as river system engineers. *Earth Surface Processes and Landforms*, 39(1), 4–25. Available from: https://doi.org/10.1002/esp.3397

Harris, H.M. & Hill, C. (2021) A place for viruses on the tree of life. *Frontiers in Microbiology*, 11, 604048. Available from: https://doi.org/10.3389/fmicb.2020.604048

Hazen, R.M. (2019) An evolutionary system of mineralogy: proposal for a classification of planetary materials based on natural kind clustering. *American Mineralogist*, 104(6), 810–816. Available from: https://doi.org/10.2138/am-2019-6709CCBYNCND

Hazen, R.M., Papineau, D., Bleeker, W., Downs, R.T., Ferry, J.M., McCoy, T.J., et al. (2008) Mineral evolution. *American Mineralogist*, 93(11-12), 1693–1720. Available from: https://doi.org/10.2138/am.2008.2955

Hazen, R.M. & Sverjensky, D.A. (2010) Mineral surfaces, geochemical complexities, and the origins of life. *Cold Spring Harbor Perspectives in Biology*, 2(5), a002162. Available from: https://doi.org/10.1101/cshperspect.a002162

Hendry, A.P. (2017) *Eco-evolutionary dynamics*. Princeton, NJ, USA: Princeton University Press.

Hendry, A.P. (2019) A critique for eco-evolutionary dynamics. *Functional Ecology*, 33(1), 84–94. Available from: https://doi.org/10.1111/1365-2435.13244

Higgins, J.A., Blättler, C.L., Lundstrom, E.A., Santiago-Ramos, D.P., Akhtar, A.A., Crüger Ahm, A.S., et al. (2018) Mineralogy, early marine diagenesis, and the chemistry of shallow-water carbonate sediments. *Geochimica et Cosmochimica Acta*, 220, 512–534. Available from: https://doi.org/10.1016/j.gca.2017.09.046

Hu, C.K. & Hoekstra, H.E. (2017) *Peromyscus* burrowing: a model system for behavioral evolution. *Seminars in Cell & Developmental Biology*, 61, 107–114. Available from: h 10.1016/j.semcdb.2016.08.001.

Huggett, R.J. (1995) *Geoecology: an evolutionary approach*. London: Routledge.

Hutton, J. (1788) Theory of the earth. *Transactions of the Royal Society of Edinburgh*, 1(2), 209–305. Available from: https://doi.org/10.1017/S0080456800029227

Hystad, G., Morrison, S.M. & Hazen, R.M. (2019) Statistical analysis of mineral evolution and mineral ecology: the current state and a vision for the future. *Applied Computing and Geosciences*, 1, 100005. Available from: https://doi.org/10.1016/j.acags.2019.100005

Jablonka, E. & Lamb, M.L. (2005) *Evolution in four dimensions. Genetic, epigenetic, behavioural, and symbolic variation in the history of life*. Cambridge, Massachusetts: MIT Press.

Johnson, D.L. (2002) Darwin would be proud: bioturbation, dynamic denudation, and the power of theory in science. *Geoarchaeology*, 17(1), 16–40. Available from: https://doi.org/10.1002/gea.10001

Jones, C.G. (2012) Ecosystem engineers and geomorphic signatures in landscapes. *Geomorphology*, 157, 75–87. Available from: https://doi.org/10.1016/j.geomorph.2011.04.039

Jones, C.G., Lawton, J.H. & Shachak, M. (1994) Organisms as ecosystem engineers. *Oikos*, 69(3), 373–386. Available from: https://doi.org/10.2307/3545850

Kim, D. & Lee, K. (2022) Landforms as combined expressions of multiple reciprocally interacting species: refining the ecosystem engineering concept. *Earth-Science Reviews*, 104152. Available from: https://doi.org/10.1016/j.earscirev.2022.104152

Knoll, A.H. (2003) Biomineralization and evolutionary history. *Reviews in Mineralogy and Geochemistry*, 54(1), 329–356. Available from: https://doi.org/10.2113/0540329

Koga, Y., Kyuragi, T., Nishihara, M. & Sone, N. (1998) Did archaeal and bacterial cells arise independently from noncellular precursors? A hypothesis stating that the advent of membrane phospholipid with enantiomeric glycerophosphate backbones caused the separation of the two lines of descent. *Journal of Molecular Evolution*, 46(1), 54–63. Available from: https://doi.org/10.1007/pl00006283

Koonin, E.V. & Martin, W. (2005) On the origin of genomes and cells within inorganic compartments. *Trends in Genetics*, 21(12), 647–654. Available from: https://doi.org/10.1016/j.tig.2005.09.006

Laland, K., Matthews, B. & Feldman, M.W. (2016) An introduction to niche construction theory. *Evolutionary Ecology*, 30(2), 191–202. Available from: https://doi.org/10.1007/s10682-016-9821-z

Laland, K.N., Odling-Smee, F.J. & Feldman, M.W. (1999) Evolutionary consequences of niche construction and their implications for ecology. *Proceedings of the National Academy of Sciences of the USA*, 96, 10242–10247. Available from: https://doi.org/10.1073/pnas.96.18.1024

Laland, K.N., Odling-Smee, J. & Gilbert, S.F. (2008) EvoDevo and niche construction: building bridges. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution*, 310(7), 549–566. Available from: https://doi.org/10.1002/jez.b.21232

Laland, K.N. & Sterelny, K. (2006) Seven reasons (not) to neglect niche construction. *Evolution*, 60(9), 1751–1762. Available from: https://doi.org/10.1111/j.0014-3820.2006.tb00520.x

Laland, K., Uller, T., Feldman, M., Sterelny, K., Müller, G.B., Moczek, A., et al. (2014) Does evolutionary theory need a rethink? *Nature*, 514(7521), 161–164. Available from: https://doi.org/10.1038/514161a

Larsen, A., Larsen, J.R. & Lane, S.N. (2021) Dam builders and their works: beaver influences on the structure and function of river corridor hydrology, geomorphology, biogeochemistry and ecosystems. *Earth-Science Reviews*, 218, 103623. Available from: https://doi.org/10.1016/j.earscirev.2021.103623

LeGeros, R. (1981) Apatites in biological systems. *Progress in Crystal Growth and Characterization*, 4(1-2), 1–45. Available from: https://doi.org/10.1016/0146-3535(81)90046-0

Lehmann, L. (2008) The adaptive dynamics of niche constructing traits in spatially subdivided populations: evolving posthumous extended phenotypes. *Evolution*, 62(3), 549–566. Available from: https://doi.org/10.1111/j.1558-5646.2007.00291.x

Lewens, T. (2019) The extended evolutionary synthesis: what is the debate about, and what might success for the extenders look like? *Biological Journal of the Linnean Society*, 127(4), 707–721. Available from: https://doi.org/10.1093/biolinnean/blz064

Lewontin, R. (1983) Gene, organism, and environment. In: Bendall, D.S. (Ed.) *Evolution: from molecules to men*. Cambridge: Cambridge University Press, pp. 273–285.

Lewontin, R.C. (2001) *The triple helix: gene, organism, and environment*. Cambridge, Massachusetts: Harvard University Press.

Lin, W., Benzerara, K., Faivre, D. & Pan, Y. (2014) Intracellular biomineralization in bacteria. *Frontiers in Microbiology*, 5, 293. Available from: https://doi.org/10.3389/fmicb.2014.00293

Lombard, J., López-García, P. & Moreira, D. (2012) The early evolution of lipid membranes and the three domains of life. *Nature Reviews Microbiology*, 10(7), 507–515. Available from: https://doi.org/10.1038/nrmicro2815

Loreau, M. (2010) *From populations to ecosystems*. Princeton University Press.

Love, A.C. (2006) Evolutionary morphology and EvoDevo: hierarchy and novelty. *Theory in Biosciences*, 124(3-4), 317–333. Available from: https://doi.org/10.1016/j.thbio.2005.11.006

Lovelock, J.E. (1979) *Gaia: a new look at life on earth*. Oxford University Press.

Mann, S. (2001) *Biomineralization: principles and concepts in bioinorganic materials chemistry*. New York: Oxford University Press.

Margulis, L. & Fester, R. (Eds). (1991) *Symbiosis as a source of evolutionary innovation: speciation and morphogenesis*. Cambridge: MIT Press.

Martin, J.B. (2017) Carbonate minerals in the global carbon cycle. *Chemical Geology*, 449, 58–72. Available from: https://doi.org/10.1016/j.chemgeo.2016.11.029

Martin, W., Baross, J., Kelley, D. & Russell, M.J. (2008) Hydrothermal vents and the origin of life. *Nature Reviews Microbiology*, 6(11), 805–814. Available from: https://doi.org/10.1038/nrmicro1991

Martin, W. & Russell, M.J. (2003) On the origins of cells: a hypothesis for the evolutionary transitions from abiotic geochemistry to chemoautotrophic prokaryotes, and from prokaryotes to nucleated cells. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 358(1429), 59–85. Available from: https://doi.org/10.1098/rstb.2002.1183

Matthews, B., De Meester, L., Jones, C.G., Ibelings, B.W., Bouma, T.J., Nuutinen, V., et al. (2014) Under niche construction: an operational bridge between ecology, evolution, and ecosystem science. *Ecological Monographs*, 84(2), 245–263. Available from: https://doi.org/10.1890/13-0953.1

Matthews, B., Narwani, A., Hausch, S., Nonaka, E., Peter, H., Yamamichi, M., et al. (2011) Toward an integration of evolutionary biology and ecosystem science. *Ecology Letters*, 14(7), 690–701. Available from: https://doi.org/10.1111/j.1461-0248.2011.01627.x

Meybeck, M. (1987) Global chemical weathering of surficial rocks estimated from river dissolved loads. *American Journal Science*, 287(5), 401–428. Available from: https://doi.org/10.2475/ajs.287.5.401

Meysman, F.J.R., Middelburg, J.J. & Heip, C.H.R. (2006) Bioturbation: a fresh look at Darwin's last idea. *Trends in Ecology & Evolution*, 21(12), 688–695. Available from: https://doi.org/10.1016/j.tree.2006.08.002

Milliman, J.D. (1993) Production and accumulation of calcium carbonate in the ocean: budget of a non-steady state. *Global Biogeochemical Cycles*, 7(4), 927–957. Available from: https://doi.org/10.1029/93GB02524

Mills, L.S.M., Soulé, M.E. & Doak, D.F. (1993) The keystone-species concept in ecology and conservation. *Bioscience*, 43(4), 219–224. Available from: https://doi.org/10.2307/1312122

Monismith, S.G. (2007) Hydrodynamics of coral reefs. *Annual Review of Fluid Mechanics*, 39(1), 37–55. Available from: https://doi.org/10.1146/annurev.fluid.38.050304.092125

Moreira, D. & López-García, P. (2009) Ten reasons to exclude viruses from the tree of life. *Nature Reviews Microbiology*, 7(4), 306–311. Available from: https://doi.org/10.1038/nrmicro2108

Morrison, S.M., Liu, C., Eleish, A., Prabhu, A., Li, C., Ralph, J., et al. (2017) Network analysis of mineralogical systems. *American Mineralogist*, 102(8), 1588–1596. Available from: https://doi.org/10.2138/am-2017-6104CCBYNCND

Müller, G.B. (2007) Evo-devo: extending the evolutionary synthesis. *Nature Reviews. Genetics*, 8(12), 943–949. Available from: https://doi.org/10.1038/nrg2219

Murdock, D.J. (2020) The 'biomineralization toolkit' and the origin of animal skeletons. *Biological Reviews*, 95(5), 1372–1392. Available from: https://doi.org/10.1111/brv.12614

Murdock, D.J. & Donoghue, P.C. (2011) Evolutionary origins of animal skeletal biomineralization. *Cells, Tissues, Organs*, 194(2-4), 98–102. Available from: https://doi.org/10.1159/000324245

Naiman, R.J., Johnston, C.A. & Kelly, J.C. (1988) Alteration of North American streams by beaver. *Bioscience*, 38(11), 753–762. Available from: https://doi.org/10.2307/1310784

Naylor, L.A., Viles, H.A. & Carter, N.E.A. (2002) Biogeomorphology revisited: looking towards the future. *Geomorphology*, 47(1), 3–14. Available from: https://doi.org/10.1016/S0169-555X(02)00137-X

Nickel, E.H. (1995) Definition of a mineral. *Mineralogical Magazine*, 59(397), 767–768. Available from: https://doi.org/10.1180/minmag.1995.059.397.20

Niklas, K.J. (1997) *The evolutionary biology of plants*. Chicago, USA: The University of Chicago Press.

Ocko, S.A., Heyde, A. & Mahadevan, L. (2019) Morphogenesis of termite mounds. *Proceedings of the National Academy of Sciences of the USA*, 116(9), 3379–3384. Available from: https://doi.org/10.1073/pnas.18187591

Odling-Smee, F.J., Erwin, D.H., Palkovacs, E.P., Feldman, M.W. & Laland, K.N. (2013) Niche construction theory: a practical guide for ecologists. *The Quarterly Review of Biology*, 88(1), 3–28. Available from: https://doi.org/10.1086/669266

Odling-Smee, F.J., Laland, K.N. & Feldman, M.W. (1996) Niche construction. *The American Naturalist*, 147(4), 641–648. Available from: https://doi.org/10.1086/285870

Odling-Smee, F.J., Laland, K.N. & Feldman, M.W. (2003) *Niche construction: the neglected process in evolution*. Princeton, USA: Princeton University Press.

Paine, R.T. (1966) Food web complexity and species diversity. *The American Naturalist*, 100(910), 65–75. Available from: https://doi.org/10.1086/282400

Pérez-Huerta, A., Coronado, I. & Hegna, T.A. (2018) Understanding biomineralization in the fossil record. *Earth-Science Reviews*, 179, 95–122. Available from: https://doi.org/10.1016/j.earscirev.2018.02.015

Perry, R.S., Mcloughlin, N., Lynne, B.Y., Sephton, M.A., Oliver, J.D., Perry, C.C., et al. (2007) Defining biominerals and organominerals: direct and indirect indicators of life. *Sedimentary Geology*, 201(1-2), 157–179. Available from: https://doi.org/10.1016/j.sedgeo.2007.05.014

Pfennig, D.W., Wund, M.A., Snell-Rood, E.C., Cruickshank, T., Schlichting, C.D. & Moczek, A.P. (2010) Phenotypic plasticity's impacts on diversification and speciation. *Trends in Ecology & Evolution*, 25(8), 459–467. Available from: https://doi.org/10.1016/j.tree.2010.05.006

Phillips, J.D. (1995) Biogeomorphology and landscape evolution: the problem of scale. *Geomorphology*, 13(1–4), 337–347. Available from: https://doi.org/10.1016/0169-555X(95)00023-X

Phillips, J.D. (2006) Evolutionary geomorphology: thresholds and nonlinearity in landform response to environmental change. *Hydrology and Earth System Sciences*, 10(5), 731–742. Available from: https://doi.org/10.5194/hess-10-731-2006

Phillips, J.D. (2008) Goal functions in ecosystem and biosphere evolution. *Progress in Physical Geography*, 32(1), 51–64. Available from: https://doi.org/10.1177/0309133308089497

Phillips, J.D. (2009a) Biological energy in landscape evolution. *American Journal of Science*, 309(4), 271–289. Available from: https://doi.org/10.2475/04.2009.01

Phillips, J.D. (2009b) Landscape evolution space and the relative importance of geomorphic processes and controls. *Geomorphology*, 109(3-4), 79–85. Available from: https://doi.org/10.1016/j.geomorph.2009.01.007

Phillips, J.D. (2016a) Landforms as extended composite phenotypes. *Earth Surface Processes and Landforms*, 41(1), 16–26. Available from: https://doi.org/10.1002/esp.3764

Phillips, J.D. (2016b) Biogeomorphology and contingent ecosystem engineering in karst landscapes. *Progress in Physical Geography*, 40(4), 503–526. Available from: https://doi.org/10.1177/030913331562464

Phillips, J.D. (2021) *Landscape evolution: landforms, ecosystems, and soils*. Elsevier.

Post, D.M. & Palkovacs, E.P. (2009) Eco-evolutionary feedbacks in community and ecosystem ecology: interactions between the ecological theater and the evolutionary play. *Philosophical Transactions of the Royal Society B*, 364(1523), 1629–1640. Available from: https://doi.org/10.1098/rstb.2009.0012

Reijmer, J.J. (2021) Marine carbonate factories: review and update. *Sedimentology*, 68(5), 1729–1796. Available from: https://doi.org/10.1111/sed.12878

Schidlowski, L. (1988) A 3,800-million-year isotopic record of life from carbon in sedimentary rocks. *Nature*, 333(6171), 313–318. Available from: https://doi.org/10.1038/333313a0

Schwab, D.B. & Moczek, A.P. (2021) Evo-devo and niche construction. In: *Evolutionary developmental biology: a reference guide placeholder text*, pp. 1179–1192. Available from: https://doi.org/10.1007/978-3-319-32979-6_46

Smith, C.H. (1986) A contribution to the geographical interpretation of biological change. *Acta Biotheoretica*, 35(4), 229–278. Available from: https://doi.org/10.1007/BF00047097

Sojo, V., Herschy, B., Whicher, A., Camprubi, E. & Lane, N. (2016) The origin of life in alkaline hydrothermal vents. *Astrobiology*, 16(2), 181–197. Available from: https://doi.org/10.1089/ast.2015.1406

Spalding, M.D., Ravilious, C. & Green, E.P. (2001) *World atlas of coral reefs*. Berkeley: University of California Press.

Spencer, C.J., Davies, N.S., Gernon, T.M., Wang, X., WJ, M.M., Rae, I., et al. (2022) Composition of continental crust altered by the emergence of land plants. *Nature Geoscience*, 1–6. Available from: https://doi.org/10.1038/s41561-022-00995-2

Stallins, J.A. (2006) Geomorphology and ecology: unifying themes for complex systems in biogeomorphology. *Geomorphology*, 77(3-4), 207–216. Available from: https://doi.org/10.1016/j.geomorph.2006.01.005

Stallins, J.A. & Corenblit, D. (2018) Interdependence of geomorphic and ecologic resilience properties in a geographic context. *Geomorphology*, 305, 76–93. Available from: https://doi.org/10.1016/j.geomorph.2017.09.012

Steiger, J. & Corenblit, D. (2012) The emergence of an 'evolutionary geomorphology? *Central European Journal of Geosciences*, 4(3), 376–382. Available from: https://doi.org/10.2478/s13533-011-0075-6

Stencel, A. & Wloch-Salamon, D.M. (2018) Some theoretical insights into the hologenome theory of evolution and the role of microbes in speciation. *Theory in Biosciences*, 137(2), 197–206. Available from: https://doi.org/10.1007/s12064-018-0268-3

Sultan, S.E. (2015) *Organism and environment: ecological development, niche construction, and adaption*. USA: Oxford University Press.

Szathmáry, E. (2015) Toward major evolutionary transitions theory 2.0. *Proceedings of the National Academy of Sciences U. S. a*, 112(33), 10104–10111. Available from: https://doi.org/10.1073/pnas.142139811

Szathmáry, E. & Maynard Smith, J. (1995) The major evolutionary transitions. *Nature*, 374(6519), 227–232. Available from: https://doi.org/10.1038/374227a0

Tambutté, S., Holcomb, M., Ferrier-Pagès, C., Reynaud, S., Tambutté, É., Zoccola, D., et al. (2011) Coral biomineralization: from the gene to the environment. *Journal of Experimental Marine Biology and Ecology*, 408(1-2), 58–78. Available from: https://doi.org/10.1016/j.jembe.2011.07.026

Torday, J.S. (2016) The cell as the first niche construction. *Biology*, 5(2), 19. Available from: https://doi.org/10.3390/biology5020019

Torday, J.S. & Miller, W.B. (2016) Phenotype as agent for epigenetic inheritance. *Biology*, 5(3), 30. Available from: https://doi.org/10.3390/biology5030030

Turner, J.S. (2000) *The extended organism: the physiology of animal-built structures*. Cambridge: Harvard University Press.

Turner, J.S. (2004) Extended phenotypes and extended organisms. *Biology and Philosophy*, 19(3), 327–352. Available from: https://doi.org/10.1023/B:BIPH.0000036115.65522.a1

Van Nuland, M.E., Wooliver, R.C., Pfennigwerth, A.A., Read, Q.D., Ware, I.M., Mueller, L., et al. (2016) Plant-soil feedbacks: connecting ecosystem ecology and evolution. *Functional Ecology*, 30(7), 1032–1042. Available from: https://doi.org/10.1111/1365-2435.12690

Viles, H.A. (Ed). (1988) *Biogeomorphology*. Oxford, UK: Blackwell.

Viles, H. (2011) Biogeomorphology. In: Gregory, K.J. & Goudie, A.S. (Eds.) *The SAGE handbook of geomorphology*. Sage, pp. 246–259. Available from: https://doi.org/10.4135/9781446201053.n14

Viles, H.A. (2012) Microbial geomorphology: a neglected link between life and landscape. *Geomorphology*, 157-158, 6–16. Available from: https://doi.org/10.1016/j.geomorph.2011.03.021

Viles, H.A. (2020) Biogeomorphology: past, present and future. *Geomorphology*, 366, 106809. Available from: https://doi.org/10.1016/j.geomorph.2019.06.022

Viles, H.A., Goudie, A.S. & Goudie, A. (2020) Ants as geomorphological agents: a global assessment. *Earth-Science Reviews*, 213, 103469. Available from: https://doi.org/10.1016/j.earscirev.2020.103469

Vogel, S. (2020) *Life in moving fluids: the physical biology of flow-revised and expanded second edition*. Princeton, New Jersey: Princeton University Press.

Wächtershäuser, G. (2003) From pre-cells to Eukarya—a tale of two lipids. *Molecular Microbiology*, 47(1), 13–22. Available from: https://doi.org/10.1046/j.1365-2958.2003.03267.x

Wagner, D.O. & Aspenberg, P. (2011) Where did bone come from? An overview of its evolution. *Acta Orthopaedica*, 82(4), 393–398. Available from: https://doi.org/10.3109/17453674.2011.588861

Ware, I.M., Fitzpatrick, C.R., Senthilnathan, A., Bayliss, S.L.J., Beals, K.K., Mueller, L.O., et al. (2019) Feedbacks link ecosystem ecology and evolution across spatial and temporal scales: empirical evidence and future directions. *Functional Ecology*, 33(1), 31–42. Available from: https://doi.org/10.1111/1365-2435.13267

Weber, J.N. & Hoekstra, H.E. (2009) The evolution of burrowing behaviour in deer mice (genus *Peromyscus*). *Animal Behaviour*, 77(3), 603–609. Available from: https://doi.org/10.1016/j.anbehav.2008.10.031

Weber, J.N., Peterson, B.K. & Hoekstra, H.E. (2013) Discrete genetic modules are responsible for complex burrow evolution in *Peromyscus* mice. *Nature*, 493(7432), 402–405. Available from: https://doi.org/10.1038/nature11816

West, S.A., Fisher, R.M., Gardner, A. & Kiers, E.T. (2015) Major evolutionary transitions in individuality. *Proceedings of the National Academy of Sciences of the USA*, 112(33), 10112–10119. Available from: https://doi.org/10.1073/pnas.1421402112

West-Eberhard, M.J. (2003) *Developmental plasticity and evolution*. Oxford University Press.

Wilkinson, M.T., Richards, P.J. & Humphreys, G.S. (2009) Breaking ground: pedological, geological, and ecological implications of soil bioturbation. *Earth Science Reviews*, 97(1-4), 257–272. Available from: https://doi.org/10.1016/j.earscirev.2009.09.005

Williams, G.C. (1996) *Adaptation and natural selection: a critique of some current evolutionary thought*. Princeton, New Jersey: Princeton University Press.

Wright, J.P., Jones, C.G., Boeken, B. & Shachak, M. (2006) Predictability of ecosystem engineering effects on species richness across environmental variability and spatial scales. *Journal of Ecology*, 94(4), 815–824. Available from: https://doi.org/10.1111/j.1365-2745.2006.01132.x

Zeebe, R.E. & Westbroek, P. (2003) A simple model for the CaCO3 saturation state of the ocean: the "Strangelove," the "Neritan," and the "Cretan" ocean. *Geochemistry, Geophysics, Geosystems*, 4(12), 1–26. Available from: https://doi.org/10.1029/2003GC000538

Zilber-Rosenberg, I. & Rosenberg, E. (2008) Role of microorganisms in the evolution of animals and plants: the hologenome theory of evolution. *FEMS Microbiology Reviews*, 32(5), 723–735. Available from: https://doi.org/10.1111/j.1574-6976.2008.00123.x

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