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Landforms as extended composite phenotypes

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ABSTRACT: Biotic influences on geomorphology (and vice-versa) are ubiquitous. This paper explores whether landforms may be extended (composite) phenotypes of biota, based on four criteria: process–form relationships between biota and landforms; evolutionary synchrony; selective pressure via ecosystem engineering and niche construction; and positive feedback benefitting the engineer organism(s). Coral reefs, peat bogs, biomantles, insect mounds, grassland soils, salt marshes, mangrove swamps, and some vegetation-dependent sand dune types clearly meet these criteria. Karst landforms, meandering rivers, and tree uprooting pit-mound systems meet the first three criteria, but positive feedback to engineer organisms has not been established. Research in biogeomorphology will surely identify other extended phenotypes. Implications are that biological evolution will continue to drive landscape metamorphosis, the appearance of new landform types, and presumably the disappearance of extended phenotypes associated with extinct species. Independently of extended phenotypes, tightly-coupled geomorphological–ecological interactions such as coevolution, and biogeomorphic forms of ecosystem engineering and niche construction are common. The toposphere, encompassing Earth's landforms, is partly a biotic construct. Some elements would be present in an abiotic world, but the toposphere would not exist in anything resembling its contemporary state without a biosphere. This raises important questions with respect to Earth system evolution. The bio, litho-, atmo-, hydro-, topo-, and pedospheres coevolve at the global scale. Major biotic events have driven revolutions in the other spheres, but the atmosphere and the global hydrological system seem to have been relatively steady-state at the global scale. The toposphere and pedosphere have not. This suggests that perhaps landforms and soils provide the major mechanisms or degrees of freedom by which Earth responds to biological evolution. Landforms and soils may thus be the 'voice' of the biosphere as it authors planetary change, even if clear biotic signatures are lacking. Copyright © 2015 John Wiley & Sons, Ltd.

KEYWORDS: biogeomorphology; niche construction; extended phenotype; biogenic landforms; toposphere

Introduction

This paper will explore the notion that Earth's landforms and landscapes are an expression of the cumulative impacts of the biosphere on surface processes. If landforms are expressions of biological evolution, rather than, or in addition to, being simply influenced by organisms, this has weighty implications for understanding the evolution of landforms, and of Earth systems in general.

Landforms reflect the combined, interacting influences of (at least) geology, climate, and time as well as biota, and of secondary, composite products of those interactions, such as soils and biogeochemical cycles. Others have argued that there is no singular, distinct topographic imprint of life – that is, that no particular topographic feature or pattern can be unequivocally related to biological effects, such that it could not form by any other means (Dietrich and Perron, 2006). Beyond the fact that distinct topographic signatures of life may yet be identified (as Dietrich and Perron (2006) acknowledged, and Bertoldi *et al.* (2011) and Corenblit *et al.* (2011) indicated for the case of vegetation along a braided river), topography is only one aspect of landforms. Others include composition, structure or morphology, longevity or lifespan, and trends or trajectories of change. Recognizing this, recent work has sought to identify geomorphic signatures of life other than topography, such as rock surface characteristics, weathering products, and regolith properties (Gorbushina *et al.*, 2002; Phillips, 2009a; Raven and Giordano, 2009).

Identification and description of landforms on the basis of topography alone (or, for that matter, on the basis of any single property) is generic; in most cases we prefer and strive for genetic descriptions. For example, a topographic pit or depression is a generic landform, while identifying it as a tree uprooting pit, a karst depression, a deflation hollow, or a buffalo wallow is a genetic description. Equifinality is common in geomorphology, whereby different processes, environmental controls, or histories can lead to very similar forms, in terms of both morphology and spatial or statistical patterns (Culling, 1987; Beven, 1996; Phillips, 1997). Thus, identifying a unique topographic signature of any given process, biotic or otherwise, is not always straightforward. While topographic information is the most readily obtained (especially in this era of LiDAR, terrestrial laser scanning, structure-from-motion photography, etc.), and often the only information for other planets, topography is only part of what landforms are.

I have previously made the case that soils are extended composite phenotypes (Phillips, 2009a). Extending the argument to landforms, however, is not simply a matter of arguing by analogy or relying on the close relationships between landforms and soils. Tightly coupled soil–biotic interactions have been recognized and studied for much longer than the reciprocal relationships between landforms and organisms. Further, there are plausible cases for completely abiotic landforms, while it is difficult to make a similar case for (Earth) soils. Thus, I will examine the case independently from the earlier argument, though some overlap is inevitable.

Background

It is axiomatic that many landforms and geomorphic processes are strongly influenced by biota, that geomorphological and ecological processes are often closely intertwined, and that landforms and surface processes are key components of the ecological framework for many organisms. Tight coupling and reciprocal interactions that transcend mutual influences, such that landforms and biota (from individuals to communities) develop interdependently, have also become widely recognized in recent years (Stallins, 2006; Corenblit *et al.*, 2007, 2008, 2011; Cotterill *et al.*, 2011; Fei *et al.*, 2014).

Second, we can stipulate that some landforms – for instance volcanic features, dunes in hyperarid deserts, or glacial scours – are created independently of any significant direct biological influences. However, a third stipulation is that even abiotic landforms are acted upon by climate, and that Earth's climate is inextricably linked to the biosphere. Thus, nothing in Earth's surface or near-surface environment is totally unaffected, at least indirectly, by the biosphere.

The stipulations above are widely, if not universally, agreed upon by geoscientists, but do not necessarily imply landforms as expressions of biota. The latter is tied to the concept of the extended phenotype. Phenotypes are the genetic expression evident in an organism's body. Dawkins (1982) introduced the idea of the extended phenotype, which includes all the effects of genes on the environment, through the behavior or actions of an organism. Specifically, this implies that alleles favoring the geomorphic (or other environmental modifications) are selected for. The extended phenotype concept differs from general environmental impacts of biota in that the former should benefit the selection of the organism's genes. Some of the more obvious examples are geomorphic, such as ant and termite mounds and beaver dams. Thus, Dawkins (1982) maintained that organisms and their biotopes (his examples include several geomorphic features) may mutually define and construct each other. Phillips (2009a) expanded this to the notion of extended composite phenotypes (ECP), noting that some soils and soil properties represent biotopes of multiple organisms. Some Mollisol/Chernozem soils, for example, are extended phenotypes of both grasses and earthworms, and soil biomantles more generally may be ECPs of multiple organisms (Phillips, 2009a). Coral reefs also involve multiple organisms and can be considered ECP.

Dawkins (1982, 2004) defends a strict definition of extended phenotypes (EP) based on the role of the biotope in increasing the representation of specific alleles (sources of genetic variation). Thus, a beaver dam, for example, does not represent an EP simply because it improves habitat and increases the likelihood of survival and reproduction of the beaver – it must also result in preferential selection of superior dam-building genes. Others (Laland, 2004; Phillips, 2009a) promote a slightly broader version, requiring only that the EP promote persistence and growth of specific species, rather than variations within species. Matthews *et al.* (2014) and Laland *et al.* (2005) prefer the concept of niche construction, which requires only ecological selection (filtering) rather than selection at the genetic level. However, niche construction does not necessarily produce features such as landforms that are expressions of specific (groups of) organisms. Rather than address the details of this debate, which largely centers on the role of alleles, genes, and individuals as agents of selection (Dawkins, 2004; Laland, 2004), or add more terminology, here I simply acknowledge a *sensu lato* version of the extended phenotype (biogeomorphic features that are expressions of an organism's activities and that promote the replication of its genes) versus the *sensu stricto* extended phenotype of Dawkins (2004). This preserves the notion of landforms as biotic expressions without requiring proof at the genetic level.

Figure 1 illustrates the relationship between biogeomorphic impacts and extended phenotypes. To be considered biogeomorphic, biotic effects on the abiotic environment must result in landforms or geomorphic features directly linked to the biotic activity. Further, these effects must result in ecological filtering; differentially affecting habitat suitability and/or resource available for different taxa. If this test is met, this constitutes biogeomorphic ecosystem engineering. If the biogeomorphic engineering preferentially benefits the engineer organism(s), then it can be construed as active, positive niche construction, and as an extended phenotype in the slightly weaker sense. If these effects can also be shown to result in increased

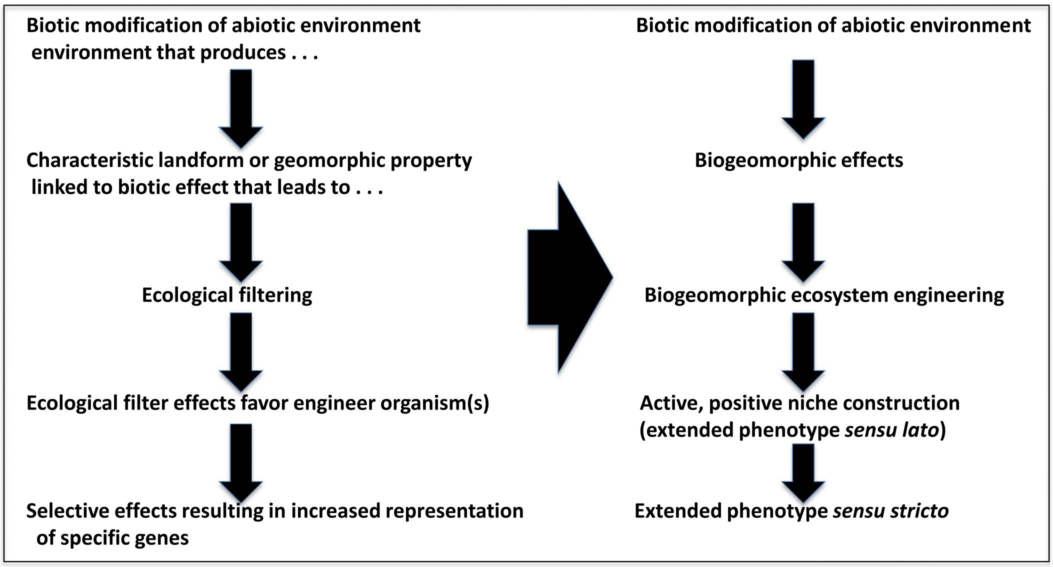

Figure 1. Relationships between biogeomorphic effects, ecosystem engineering, and extended phenotypes.

representation of specific genes, it meets the test for extended phenotypes *sensu stricto*. In some arid and semi-arid environments, for example, vertical redistribution of water and minerals by tree roots results in the formation of dense clay layers or clay pavements. These inhibit root penetration by other plants, thus increasing resource availability for the engineer tree (Verboom *et al.*, 2013). This clearly favors the replication of the engineer trees, and it is not unlikely that superior clay-forming genes are favored by selection. However, the clay layers clearly represent an extended phenotype of the tree in (at least) the broad definition used here.

Because the time scales of both biological and landform evolution usually preclude direct observation of development or coevolution (the latter defined here as contemporaneous development of biota and landforms characterized by mutual feedbacks), four tests are necessary to make a strong argument for landforms as extended phenotypes:

1. *Process-form relationships*: it must be demonstrated that actions of one or more organisms can create or strongly influence the development and characteristics of a landform.
2. *Synchrony*—the landform and biota must have developed contemporaneously. Specifically, the landform purported to be a phenotype cannot appear in the paleoenvironmental record before the organism(s). In the case of some genetic landforms this test is easily, though tautologically, passed. For example, pit-mound systems associated with tree uprooting cannot have existed before the evolution of woody plants, though other sorts of pit-mound pairs could have.
3. *Selective pressure*—the landform must create environmental conditions that comparatively (dis)advantage specific organisms.
4. *Positive feedback*--the selective pressure must favor the organism(s) associated with creation of the landform in question.

Passing tests 1–3 does not demonstrate landforms as EP, but does indicate the processes of ecological or ecosystem engineering and niche construction. Ecosytem engineer organisms have a disproportionate influence on the abiotic environment relative to their numbers (Jones *et al.*, 1994, 1997; Jones, 2012). The counterpart of ecosystem engineering in evolutionary biology is niche construction, the processes whereby engineer organisms alter the environment (for themselves and/or other species) and thereby influence selective pressures (Odling-Smee *et al.*, 2003; Matthews *et al.*, 2014). Niche construction may be active or passive (i.e. selective effects on either the engineer organism or on other species) and positive or negative (i.e. benefiting or detrimental to the engineer species). Extended phenotypes imply active, positive niche construction. Explicit discussions of ecosystem engineering and niche construction in a geomorphological context are given by Corenblit *et al.* (2008; 2010; 2011), Jones (2012), and Fei *et al.* (2014). Table I summarizes some of the key concepts related to biotic–abiotic interactions referred to above, while Table II indicates a range of biotic influences on landforms and geomorphic processes and their relationships to ecosystem engineering, niche construction, and extended phenotypes.

In the next section, a number of examples of potential extended phenotype landforms will be examined.

Biogenic Landforms

The examples in this section represent landforms known to have strong biotic influences and biotic–abiotic feedbacks, which will be considered with respect to whether they represent EP. These examples are illustrative, not comprehensive. Some landforms, such as mima mounds, may be biogenic, abiotic, or a combination (Burnham and Johnson, 2012). In cases where these mounds are created by burrowing fauna to enhance habitat suitability and increase survivability, they seem to meet the EP definition. However, because of the polygenetic nature of the mounds (and debate about the formation of specific mima mound areas), one cannot make global statements about their genesis (Burnham and Johnson, 2012).

Temporally, impacts must transcend at least two generations of the organism to have any habitat or selection effects. Also note that the examples focus on landforms at the meter scale or larger. A number of smaller geomorphic phenomena, which might be considered landforms at certain scales, are biogenic (e.g. many iron oxide features; Fortin and Langley, 2005; Colombo *et al.*, 2014). While organisms responsible for EP, ECP, and niche construction may range from microbes to elephants, impacts are not necessarily proportional to size of individuals (e.g. peat bogs and coral reefs are larger than elephant wallows; and the total area/mass impacted by ants or termites may be much greater than that of, say, hippopotami or redwood trees). More work remains to be done on the scale dimensions of biogeomorphic feedbacks.

Geomorphic phenomena created by organisms meet the process-form criterion by definition, and must also meet the synchrony criterion, though sometimes biogeomorphic effects may be manifest with a single generation of an organism (e.g. faunal burrows), and other times with multiple generations (e.g. mollic horizons, stromatolites). The key questions in these cases are thus selective pressure and positive feedback.

Coral reefs clearly meet these criteria (Spencer and Viles, 2002; Hopley *et al.*, 2007; Bourillot *et al.*, 2009). Reef formation and growth strongly influences bathymetry, water depth, substrate, light, and water circulation, creating a mosaic of distinctive habitats. These selection effects are obvious in terms of ecological filtering, and are also reflected on longer time scales in the evolution of reef-building organisms and associated reef species (Pormar and Hallock, 2007; Bourillot *et al.*, 2009; Huntington and Liman, 2012; Briggs and Bowen, 2013). Recent work also shows mechanistic evidence of positive niche construction, with coral effects on local boundary-layer turbulence enhancing the organisms’ ability to exchange nutrients and dissolved gases (Shapiro *et al.*, 2014).

Peatlands also meet the extended composite phenotype criteria. Their development exerts selection effects via hydroperiod and moisture regimes and related biogeochemical circumstances (e.g. pH, anoxia, anaerobic and reducing conditions), nutrient cycling, and substrate. Because the dominant peat-forming plants are well adapted to the created environment, while plants more generally are not, strong positive feedback is present (cf. Calder and Gibling, 1994; Bragg and Tallis, 2001; Evans and Warburton, 2008).

Peat bogs and coral reefs are formed by, and composed of the remains of, interrelated organisms. Another class of biogenic landforms involves features formed by organisms in or from inorganic materials. Biomantles are surficial layers of regolith created by the actions of bioturbating species (Johnson, 1990; Johnson *et al.*, 2005). Though in some cases the biomantle may be the result of a single species, in many instances multiple species are involved. The process–form relationships are established for biomantles, and synchrony can be assumed (and is evident in the paleosol evidence; Brown and Kraus, 1993; Retallack, 2001, 2004a). Selective pressure occurs via the edaphic properties of the biomantles. Positive feedbacks are also present in many cases; the most compelling example is biomantles created by earthworms (Laland, 2005; Jouquet *et al.*, 2006; Nuutinen, 2011).

Other biogenic landforms include termite and ant mounds, and pit-mound pairs created by tree uprooting. As these

Table I. Summary of some key concepts

Concept	Definition	Examples	References
Extended phenotype	Organism genes expressed through effects on the environment	Ant and termite mounds, beaver ponds, burrows and nests	Dawkins, 1982; Jouquet *et al.*, 2006
Extended composite phenotype	Environmental phenomena reflecting the combined, interacting genetic expressions of multiple species	Soils	Phillips, 2009a; Crawford *et al.*, 2012
Ecosystem engineering	Biotic modifications of the environment that improve habitat for the engineer or other species	Numerous weathering, bioconstruction, and sedimentation phenomena in geomorphology	Jones *et al.*, 1994; Jones, 2012; Corenblit et al., 2008; 2011; Fei *et al.*, 2014
Niche construction	Environmental impacts of organisms that improve habitat and evolutionary fitness for the engineer species (active) or for other species (passive)	Woody vegetation and riverine and riparian habitats and landforms	Odling-Smee *et al.*, 2003; Griffiths, 2005; Corenblit *et al.*, 2011; Matthews *et al.*, 2014

Table II. Range of biotic impacts on landforms and geomorphic processes, and relationship to biogeomorphic ecosystem engineering, niche construction, and extended phenotypes

Degree of biotic impact	Description	Examples	Biogeomorphic feedbacks
1. Negligible	No significant direct biotic effects	Hyperarid sand dunes, glacial scours, lava flows	None
2. Indirect	Biota influence rates or frequency of processes that would occur anyway	Effects of vegetation cover on erosion and sedimentation	May constitute ecosystem engineering and niche construction
3. Biotically mediated	Biota or biotic by-products drive geomorphic processes	Some forms of chemical weathering; karst formation; tree uprooting pits and mounds	May constitute ecosystem engineering and niche construction
4. Biogenic	Landforms constructed by direct, purposeful activities of biota from other mineral or organic materials	Ant and termite mounds, beaver dams/ ponds, faunal dens and burrows	Active, positive niche construction and extended phenotypes
5. Biogenic-organic	Landforms constructed by biota and composed mainly of remains of the constructing organisms	Coral reefs, peat bogs	Active, positive niche construction and extended phenotypes

landforms are defined genetically, the process–form and synchrony criteria are obviously met, and the environment–habitat modifications and resulting selective effects are well known. The positive feedback effects are also established in some cases – for instance, Dawkins (1982) uses ant and termite mounds to illustrate the extended phenotype concept. The different local habitats created by tree uprooting pit mounds favor specific soil faunal and microbial communities (Nachtergale *et al.*, 2002; Lohmus *et al.*, 2010; Kooch *et al.*, 2013, 2014) and different tree species may establish on pits vs. mounds (Sebkova *et al.*, 2012). However, in this case the positive feedback to the uprooted species has not been shown.

Microbially induced landforms

Some of the earliest life on Earth was in the form of microbial mats. Some of these, particularly cyanobacteria, are capable of producing microbially-induced sedimentary structures and landforms, which must be considered Earth's oldest biogenic landforms (Noffke, 2009). Mucus secretions trap mineral grains, or in some cases debris, that is cemented by calcium carbonates. This may result in stromatolite landforms and reefs. The accreted or precipitated material provides shelter and protection to the engineer microbes. Thus stromatolite formation represents biogeomorphic niche construction that has been occurring since the Archean, and the features are expressions of the microbial genes. Viles (2012) describes similar microbially constructed landforms, which are active at present.

Plants and meandering rivers

Except in very cohesive materials, fluvial channels cannot maintain a stable, single-thread meandering channel in the absence of vegetation. Without the increased bank resistance associated with plants, channels assume a braided planform. This general relationship and the associated process–form mechanics have been established via empirical studies, laboratory experiments, and simulation modeling (Davies and Gibling, 2010, 2013; Crosato and Saleh, 2011; Gurnell, 2014). Other studies have shown more specific, detailed relationships between vegetation communities and fluvial channel morphology (Corenblit *et al.*, 2009; Francis *et al.*, 2009; Yu *et al.*, 2014).

The sedimentary record establishes synchrony. Alluvial deposits older than the establishment of vascular plants in the early Paleozoic overwhelmingly represent anabranching (including braided) styles (Davies and Gibling, 2010, 2013). The appearance of alluvial architecture and sedimentary structures associated with single-channel meandering rivers coincides with or postdates the fossil record of vascular plants.

Meandering rivers create particular habitats and environmental conditions involving substrate type and mobility, hydroperiods, light availability, and other conditions that strongly influence vegetation, and numerous examples exist of plants closely adapted to specific geomorphic settings such as point bars, natural levees, and oxbows (Rood *et al.*, 2011). Thus, at least passive niche construction is at work. It seems clear that vegetation enables the formation of single-channel systems, and that this ecosystem engineering and niche construction exerts selective pressure. However, it is more difficult to establish direct positive feedback relationships to specific taxa, as opposed to vascular plants more generally.

Grassland soils

The notion of soils as extended composite phenotypes is outlined elsewhere (Phillips, 2009a). However, the example of certain types of soils characteristic of subhumid grasslands is worthy of brief mention here because the coevolution of plants, animals, and soil is well established in this case. The soils in question are characterized by dark, soft, organic-rich surface horizons with relatively high base saturation, and are often classified as Chernozems or Mollisols (in the US Soil Taxonomy). Dokuchaev (1883) showed that Russian Chernozems have specific morphological properties attributable to vegetation, organic matter, and earthworms, regardless of the parent material or geological context. Much later, others (Retallack, 2001, 2004b) demonstrated that grassland soils coevolved over the past 40 ma with grasses and herbivores.

The process–form relationships, synchrony, selection, and feedbacks are particularly well established in the stratigraphic record of North America. The appearance of grasses is synchronous with paleosols representing new grassland pedotypes in the Eocene. Paleosol and other paleontological evidence shows emergence of soils associated with bunch and sod grassland, and sagebrush coincident with the appearance of the vegetation types at various times between 39 and 6 ma. Further, paleosols reflect the coevolution of vegetation communities and mammalian fauna (Brown and Kraus, 1993; Retallack, 1994, 2004a, 2004b, 2007).

While these soils seem to meet the weaker version of EP, it is not clear that their formation and evolution favors specific organisms or species (as opposed to, for example, general vegetation habits or physiognomy), much less genes.

Coastal wetlands

Salt marshes and mangrove swamps are landforms and ecosystems where geomorphological, hydrological, and ecological processes are inextricably intertwined. Feedbacks among geomorphological processes (especially sediment deposition), edaphic conditions for vegetation (hydroperiod, salinity, and substrate stability), and plant-driven processes (principally sediment trapping and organic matter accumulation) are essential to both the geomorphic nature and hydroecological functions of these systems. Vegetation must be adapted to soil saturation and occasional, if not regular, inundation, high salinity, and frequent disturbances from coastal storms. Thus the selection effects and positive feedback criteria also are met.

The feedbacks between vegetation establishment and production, sediment trapping, vertical accretion, and hydrodynamic regime have long been known (Reed, 1990), but recently these phenomena have been linked to active niche construction by plants. Da Lio *et al.* (2013) argued that the continued existence of tidal marsh landforms depends on the biogeomorphic actions of salt-tolerant vegetation, with biota of tidal environments collectively termed the ‘secret gardener.’ Van Hulzen *et al.* (2007) and Bouma *et al.* (2013) have explicitly linked biogeomorphic effects to species-specific vegetation traits (Van Hulzen *et al.*, 2007; Bouma *et al.*, 2013).

Sand dunes

Some sand dune types, particularly in hyper-arid climates, are as close to a totally abiotic landform as can be found on Earth, and do not involve any direct biotic role. In his review of coastal transgressive dune systems, for example, Hesp (2013) outlined numerous developmental pathways and the role of vegetation.

For those dune forms specifically related to vegetation, the process–form links and synchrony are clear or can be assumed, respectively. Selective pressure and positive feedbacks are not as well known, though ecological filtering is clearly present. Plants must be adapted to the conditions of the dry climates or sandy coastal settings involved. Further, plants that are able to colonize sand dunes (as opposed to those that initiate or influence dune formation by sediment trapping and subsequently die off) must be able to tolerate factors such as substrate mobility, burial, and wind stress. In at least some cases biological selection effects have been shown (Maun, 2008; Zarnetske *et al.*, 2012), and the biogeomorphic ecosystem engineering and niche construction role of some dune plants has been established (Godfrey and Godfrey, 1973; Godfrey, 1977; Zarnetske *et al.*, 2012). Hence, it is likely that some sand dunes are extended phenotypes; e.g. some coastal parabolic dunes (Godfrey and Godfrey, 1973; Godfrey, 1977).

Karst

The carbonate rocks in which karst typically forms are biogenic, and organisms are critical, via respiration of CO_2, in the hydrocarbonate dissolution processes that characterize karst landscapes. No evidence of karst or paleokarst exists in the rock record before the Proterozoic. Accordingly, karst landscapes are worthy of investigation in the context of landscapes as extended composite phenotypes. At this point it is clear that organisms are critical to the development of karst landforms, and that development of these forms (especially subsurface caverns) has strong selection effects. Further, some cave-dwelling organisms enlarge their habitat by promoting dissolution (Lundberg and McFarlane, 2012). But while there exists abundant evidence for ecosystem engineering, the positive feedbacks to the engineer organisms are as yet unproven. Further, while karst development requires biota, it is not clear that any particular organisms are required.

Extended phenotypes?

All the examples discussed above (and many others) exhibit a strong role for biota in landform genesis, and organism–landform interactions. All these landforms reflect biogeomorphic ecosystem engineering. But ecosystem engineering alone does not necessarily translate to landforms as extended phenotypes.

Table III summarizes the examples from the previous section with respect to the organismal role in their formation, synchrony with respect to organism and landform appearances in the geologic record, biological selection effects arising from landform genesis, niche construction, and evidence for coevolution. Coevolution in Table III is construed not just as contemporaneous, interacting development over time, but as active biotic influences on landforms which in turn influence selection effects and fitness of organisms.

From Table III, strong arguments can be made for stromatolites, coral reefs, peat bogs, biomantles, ant and termite mounds, grassland soils, salt marshes and mangrove swamps, and some sand dunes as EP. Insect mounds, the coastal wetlands, and some dune examples (as individual features) may represent extended phenotypes of individual species, while reefs, peatlands, and grassland soils are ECP representing the combined, interacting effects of

Table III. Summary of landform examples with respect to biogenesis, synchrony of first appearances, selective pressure on the ecological engineer organism, niche construction, and evidence for coevolution. See text for more explanation. *Biogenesis key*: 1: Composed largely of remains of organisms inhabiting it; 2: Constructed by direct, purposeful action of organisms; 3: Byproduct of direct, active biotic activities; 4: Byproduct of indirect, passive, biotic influences. *Synchrony key*: 1: Exists by definition; 2: Demonstrated in the paleoenvironmental record; 3: Synchrony likely, but not yet clearly demonstrated

Landform	Biogenesis	Synchrony	Selective pressure[a]	Niche construction	Coevolution
Microbially induced landforms (e.g. stromatolites)	1, 2	1, 2	Yes	Yes	Unknown
Coral reef	1	1	Yes	Active, passive	Yes
Peat bogs and mires	1	1	Yes	Active, passive	Likely
Biomantles	1, 2, 3, 4	1	Yes	Active, passive	Yes; Likely
Ant, termite mounds	2	1	Yes	Active, presumably passive	Yes
Tree uproot pit-mounds	4	1	No	Passive	Unlikely
Meandering rivers	4	2	No	Passive	Yes
Chernozems Mollisols	1, 4	2	Yes	Active, passive	Yes
Salt marshes, mangrove swamps	1, 4	1, 3	Yes	Active, passive	Likely
Karst (caves, dolines)	3, 4	2	No	Passive	Unknown
Sand dunes[b]	4	3	In some cases	Active, passive	Likely

[a] All examples exert selection through environmental effects and habitat; yes/no refers to whether selection pressure specifically favors the formative biota.
[b] Dune forms specifically related to vegetation; e.g. parabolic, nebkhas, etc.

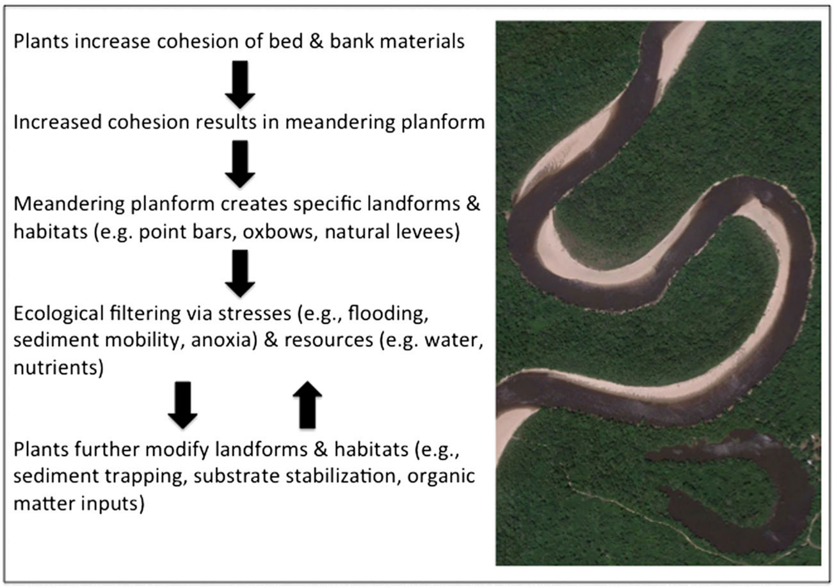

Figure 2. Biogeomorphic feedbacks in meandering alluvial rivers. Photo: Sabine River, Texas/Louisiana, USA (Google Earth™ image). This figure is available in colour online at wileyonlinelibrary.com/journal/espl

multiple species. For meandering rivers, this form can occur independently of vegetation in sufficiently cohesive materials, and the positive feedback to specific taxa is unproven. Tree uproot pit mounds and karst features are also not EP – though obviously biogenic, they are not a genetic expression of the biota involved. Figures 2 and 3 provide contrasting examples of a system with strong biogeomorphic feedbacks but no clear evidence of active, positive niche construction (meandering rivers), and one that can be considered an EP (vegetated dunes).

Since the proposal of soils as extended composite phenotypes (Phillips, 2009a), additional evidence has emerged demonstrating some of the mechanisms involved as pedogenesis exerts selective effects on organisms that in turn influence pedogenesis (Pregitzer *et al.*, 2010; Nuutinen, 2011; Crawford *et al.*, 2012; Laliberte *et al.*, 2013; Schweitzer *et al.*, 2014). Independently, Verboom and Pate (2006, 2013) developed the phytotarium concept in which plants at specific vertical layers and their associated microbial communities construct niches to maximize access to water and nutrients. Some of Verboom and Pate's (2006, 2013) empirical evidence suggests that in some cases vertical texture contrast regoliths (coarser surface layers over finer sublayers) may be biogenic beyond the bioturbation and indirect effects already known to influence vertical texture contrasts (see review by Phillips and Lorz, 2008). The role of specific trees in synthesis of pedogenetic clays, and the direct role of tree roots in redistribution of clays in the soil profile makes a strong argument that some texture-contrast profiles are extended phenotypes of tree species (Verboom and Pate, 2006, 2013; Pate and Verboom, 2009; Verboom *et al.*, 2009, 2013). A strong plant role in producing other types of 'clay pavement' phenomena in some western Australian regoliths, including laterite formation, is also shown by the same authors (Pate *et al.*, 2001; Verboom and Pate, 2003, 2013). Given Retallack's (2001) assertion that paleosols corresponding to Ultisols and Alfisols (defined by the presence of vertical texture contrasts in the form of clay-enriched subsoils) do not appear until the first fossil evidence of forest ecosystems, these plant–soil–landform interrelationships deserve more research. However, because vertical texture contrasts can also arise by dominantly or purely abiotic processes (Phillips and Lorz, 2010), this example also reinforces the difficulties raised by equifinality.

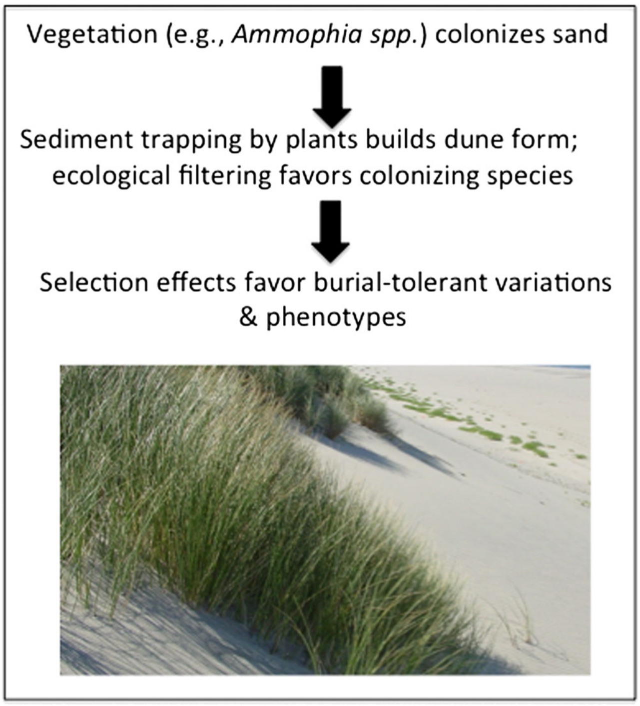

Figure 3. Dune development by ecosystem engineer plants and emergence of extended phenotype dune landform. Photo: *Ammophila arenaria* on coastal fordune in Oregon, USA. Detail from photo by P. Zarnetske (https://jecologyblog.wordpress.com/2013/06/14/indirect-effects-and-facilitation-among-native-and-non-native-species-promote-invasion-success-along-an-environmental-stress-gradient/. This figure is available in colour online at wileyonlinelibrary.com/journal/espl

Global extent

Table IV shows estimates of the areal extent of some landform types discussed above. The estimates vary in quality and precision, and the extent of these landform types varies at both human and geological time scales. However, the table clearly indicates that landforms with very strong levels of biological influence cover a substantial portion of the non-ocean planetary surface.

About 87% of Earth's land surface area is covered by soil (Table IV), and thus has at least some ECP characteristics. About 30% is forested, and accordingly potentially subject to intense biomechanical as well as biochemical impacts on weathering, regolith development, and sediment transport. Another 3% is occupied by peatlands, and about 6% by Mollisols. With 10 to 15% comprised of karst landscapes (Table IV), it is clear from these examples alone that a large proportion of the terrestrial surface of Earth is occupied by landforms with a very strong biological signature; and for some of these very strong EP or ECP arguments can be made.

Landscape Metamorphosis and Niche Construction

In geomorphology, metamorphosis refers to major, long-lasting changes in morphology and functioning of landscapes, broadly analogous to regime shifts in ecology. The term has been most commonly applied in fluvial systems, but is applicable to geomorphic systems in general. Can landscape metamorphosis occur due to biotic change and the associated ecosystem engineering? At Earth system evolution scales, major biological events such as 'great oxidation event' 2400 ma, and the Permo-Triassic extinction about 252 ma resulted in fundamental geomorphological (as well as other environmental) changes at a global scale (Knoll, 2003; Lenton and Watson, 2011). It is also clear that natural or human disturbances that, for instance, result in removal of vegetation cover (or revegetation) can radically change geomorphic process regimes and landforms. Biogenic landforms (e.g. coral reefs, peat bogs, insect mounds, etc.) can clearly be integrated into or superimposed upon existing landscapes. The question here is whether an existing landscape (e.g. a watershed, dune field, barrier island) can be altered in its entirety due to biogeomorphic ecosystem engineering.

Contemporary evidence of landscape metamorphosis driven by ecosystem engineering is provided by observations of the biogeomorphic effects of invasive or colonizing species (see review by Fei *et al.*, 2014). For example, metamorphosis of channels in the western USA has been associated with proliferation of salt cedar (*Tamarix* spp.), which involves changes in channel dimensions, width/depth ratios, and flow regimes due to effects on channel resistance, sediment trapping, and water use by the phreatophyte (Graf, 1978; Everitt, 1998).

Several examples exist of changes in coastal dune morphology due to invasion or purposeful establishment of beach grass (*Ammophila* spp.), a burial-tolerant, dune-building plant. In the case of the Outer Banks barrier island chain (North Carolina, USA), the changes included not only stabilization and growth of dunes, but also fundamental changes in barrier island morphology and washover dynamics (Dolan and Godfrey, 1973; Godfrey and Godfrey, 1973; Godfrey, 1977; Stephenson, 1990). Non-native saltmarsh cordgrass (*Spartina* spp.) has triggered landscape metamorphosis, from tidal mudflats to saltmarsh, in China (Wang *et al.*, 2006, 2012).

There are undoubtedly other examples of biogeomorphic landscape metamorphosis – the introduction of non-native species at a known time makes these cases relatively simple in terms of identifying the biogeomorphic processes and impacts involved. Also, the examples chosen are those that unequivocally illustrate metamorphosis, to avoid becoming mired in debate over whether severe impacts necessarily constitute metamorphosis, or whether the biotic effects are ecosystem engineering.

Table IV. Estimated global area of some strongly biotically influenced landform types

Landform type or environmental setting	Extent (million km^2)	Percentage, total continental surface area	Source
Coral reefs	0.28	Not applicable	WMO, 2010
Peatlands	>4	≈3	Joosten and Clarke, 2002
Karst	15 to 22	10 to 15	Ford and Williams, 2007
Soils	130	87	Eswara *et al.*, 1999
Mollisols	9.3	≈6	USDA[a]
Forest[b]	38	30	Lindquist *et al.*, 2012
Mangrove swamps	0.181	0.12	Spaulding *et al.*, 1997
Tidal marshes	0.045	0.03	Greenberg *et al.*, 2006

[a] Based on estimate of about 7% of ice-free land area from the USA Department of Agriculture, reported at http://www.cals.uidaho.edu/soilorders/mollisols.htm (last accessed 16 June 2014)

[b] Total estimated forest area as of 2005.

Evidence of biogeomorphic landscape metamorphosis on longer time scales exists in the form of two transformations already mentioned: the role of vegetation (particularly woody plants) in transforming many braided and anabranching fluvial systems to meandering streams, and the coevolution of grasses and herbivores in the development of soil and regolith covers (Retallack, 2007).

Niche construction pathways

Figure 4 is a conceptual model illustrating potential pathways of ecosystem engineering, niche construction, and landform biogenesis. Assuming a starting point of newly exposed ground, abiotic conditions and possibly biotic influences create a set of environmental controls that define habitat and potential niches. Organisms capable of exploiting or tolerating these conditions establish themselves, and begin to modify environmental conditions. In some cases these modifications maintain or reinforce existing niches, benefiting at least some of the existing species. This is the pathway of active niche construction, and development of extended (composite) phenotypes. In other cases ecosystem engineering modifies existing niches or creates new ones, favoring organisms other than the engineer species. This is the pathway of passive niche construction. The active and passive niche construction pathways correspond to the functional and residual components of landforms identified by Corenblit *et al*. (2010).

Either pathway can be reset by disturbances or environmental change (return to the top of Figure 4). The pathways can also switch. Passive niche construction may eventually facilitate establishment of active niche construction species. For instance, biotically driven speleogenesis involves passive niche construction for hypogean species. Some of these, once established, actively promote continued dissolution and cave enlargement, and therefore active niche construction (Lundberg and McFarlane, 2012). And active niche construction may not continue indefinitely even in the absence of disturbance or environmental change, as limiting thresholds are reached or as resources are depleted. For example, active niche construction in the intertidal zone by saltmarsh cordgrass (*Spartina* spp.) involves sediment trapping and vertical accretion. Ultimately this may reach an elevation such that inundation is reduced, switching to passive niche construction favoring high marsh species (Marani *et al*., 2013). Similar phenomena may occur in fluvial systems, with alluvial surfaces stabilized by vegetation eventually accreting to the point that they transform into terrestrial surfaces (Corenblit *et al*., 2009).

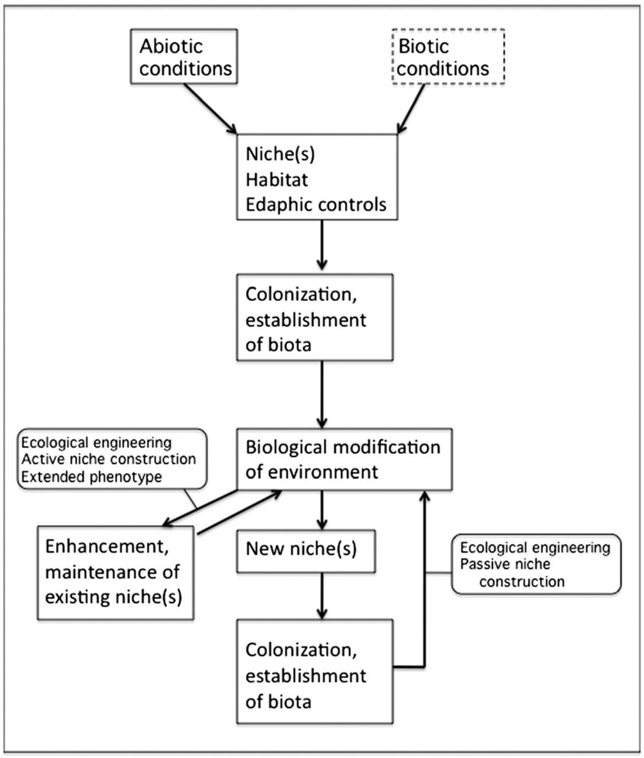

Figure 4. Biogeomorphic niche construction pathways.

Biosphere, Atmosphere, Toposphere

Vernadsky (1926), who developed the biosphere concept, conceptualized the biosphere as a planetary membrane that captures, stores, and transforms solar energy. Though the proportion captured by the biosphere is small compared with that represented by climate processes, it is large compared with other energy sources for geomorphic processes (Smil, 2008; Phillips, 2009b). If even a minuscule fraction of net primary productivity does geomorphic work (e.g. bioturbation, bioweathering, bioerosion, organic matter formation), this is (as a global average) a greater energy input for landscape evolution than geophysical processes (Phillips, 2009b). The biosphere and the soil have both been characterized as an ‘excited membrane’ or skin (Vernadsky, 1926; Nikiforoff, 1959) at the planetary surface, stimulated by solar energy inputs. Acknowledging the slower pace and longer time scales sometimes involved, is Earth’s topography also an ‘excited membrane?’

Vernadsky (1926) and many others subsequently have noted that Earth’s atmosphere is in chemical disequilibrium, its composition maintained by photosynthesis, respiration, and other biospheric processes. Organisms are not required for an atmosphere to exist, or for the existence of most atmospheric constituents. However, the atmosphere in its current general chemical composition (which has been maintained in approximate steady-state for >2 Ga) is inextricably linked to the evolution and maintenance of the biosphere. This is a central tenet of the Gaia Theory (Lovelock, 1995), though the basic biogeochemical principles are independent of Gaia. But while Earth’s atmosphere contains the signature of a biosphere, it cannot be said to represent any particular taxa.

Biotic influences on surface processes and landforms are ubiquitious, and tightly-coupled interactions reflected in biogeomorphology, ecosystem engineering, and niche construction are pervasive. At least some landforms can be considered extended (composite) phenotypes. Thus, as with the atmosphere, while Earth would have landforms in the absence of a biosphere (and of course, did before the appearance of life), and some constituents that would also exist on an abiotic surface are evident in the current situation, contemporary landforms and landscapes in their current state would not be possible without biota. Using the term toposphere to encompass the totality of Earth’s landforms (following Huggett, 1995), its general existence cannot be said to be biotically dependent. However, like the atmosphere, the toposphere would be profoundly different without the biosphere.

At least one difference is critically important in this comparison. While the atmosphere, even as species, communities, and ecosystems have been in long-term evolutionary flux, has been maintained in an approximate steady-state, no such argument has been made for landscapes on geologic time scales. Global scale revolutions since the Archean have profoundly and irreversibly changed the biosphere and toposphere – however, change in atmospheric composition, and in the general global hydrosphere, has been moderated and has not been irreversible (Lenton and Watson, 2011).

Biotic changes in the atmosphere and hydrosphere are rapidly diffused throughout those spheres due to their global interconnectivity, at velocities of fluid flows measured in m s^{-1}. By contrast, landforms and soils are interconnected at much more restricted spatial scales – subcontinental at most, and not infrequently over areas on the order of 100 m^2 or less. Further, while propagation of impacts and changes sometimes occurs at fluid velocities, other processes (e.g. weathering and denudation) have rates often measured in units of m yr^{-1} to m ma^{-1}. Thus soils and landforms have much longer response and relaxation times to biologically driven change than the atmosphere–ocean system, and impacts are local and regional rather than global. This in turn leads to one conclusion and one speculation: landforms and soils have a much richer 'memory' of biological change (independently of whatever fossils they may contain) than the other spheres. Much more speculatively, it is possible that the toposphere and pedosphere locally absorb most of the environmental effects of biota, thus buffering the atmosphere, hydrosphere, and lithosphere from major changes. Evidence exists of specific instances of feedbacks whereby geomorphic and pedologic change provides negative feedback to changes in atmosphere/hydrosphere composition. For example, biotically-driven changes in atmospheric carbon dioxide concentrations lead to climate change, which result in accelerated or decelerated silicate weathering rates, either absorbing or releasing atmospheric CO_2 (Berner, 1992; Kump *et al.*, 2000; Malkowski and Racki, 2009). However, the complex interrelationships among soils, landforms, biota, climate, hydrology, and geology make it difficult to (dis)prove this as a general principle.

Concluding Remarks

Not only topographic features, but also other aspects of landforms, such as stratigraphic layering and chemical composition, are often characterized by multiple causality. These multiple causes often include both biotic and abiotic processes. This equifinality makes it difficult to unequivocally identify or prove (a)biotic origins. Further, many landforms are polygenetic, with a combination of processes involved, which may be biological, physical, chemical, and hybrid. Perhaps the search for 'signatures' of life should be expanded to the search for the 'voice' of life. To use literary analogies, a writer's signature signifies responsibility or claims credit for authorship. A writer's voice is their style; the quality that makes his or her writing unique, and which is reflected in the tone, syntax, word choice, diction, punctuation, etc. Determining authorship of an unsigned manuscript based on the writer's voice may be a better metaphor for the problem of identifying 'authorship' of landforms than searching for a signature.

Making further progress in this area involves not only integration of geosciences and biosciences, but also of approaches to both at different time scales. Thus process and historical geomorphology, biogeography, ecology, and evolutionary biology must be linked to each other, and to stratigraphy, paleontology, and other forms of paleoenvironmental reconstruction.

Notwithstanding difficulties in attributing specific landforms to organisms, directly or indirectly, biotic influences on geomorphology (and vice-versa) are ubiquitous. Further, tightly-coupled geomorphological–ecological interactions such as coevolution and biogeomorphic forms of ecosystem engineering and niche construction are common. Thus, while identification of an unequivocal signature that might prove, for example, the existence of life on other planets has not yet been achieved, Earth's toposphere is in some sense a biotic construct. Landforms may be abiotic, and some elements of the contemporary landscape would be present in an abiotic world. However, the toposphere as a whole would not exist in anything resembling its contemporary form.

Evidence shows that some landforms and landscapes are EPs. Ongoing and future research in biogeomorphology will undoubtedly identify others. Implications are that biological evolution will continue to drive landscape metamorphosis, the appearance of new landform types, and presumably the disappearance of extended phenotypes associated with extinct species. At process geomorphology and ecological time scales, biogeomorphic changes associated with introduction of new species provide proof of concept in this regard (Fei *et al.*, 2014).

This raises some interesting questions with respect to Earth system evolution. The bio, litho-, atmo-, hydro-, topo-, and pedospheres coevolve at the global scale. Major biotic events have driven revolutions in the other spheres (Lenton and Watson, 2011), but the atmosphere and the global hydrological system seem to have been relatively steady-state at the global scale. The toposphere and pedosphere have not, and display substantially more spatial variability in responses than oceanic or atmospheric composition. This suggests that perhaps landforms and soils provide the major mechanisms or degrees of freedom by which Earth responds to biological evolution, at least within the context of the permanently oxygenated atmosphere and ocean that have existed for the past 2.4 Ga. There is some evidence to support this with respect to the carbon cycle and feedbacks among ecological processes, atmospheric and ocean chemistry, biotically-enhanced weathering, and soil and sedimentary carbon storage or release (Huggett, 1991, 1995; Lenton and Watson, 2011). Landforms and soils may thus be the 'voice' of the biosphere as it authors planetary change, even if clear biotic signatures are lacking.

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