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ESEX Commentary

Vegetation as a major conductor of geomorphic changes on the Earth surface: toward evolutionary geomorphology

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Earth Surface Processes and Landforms

ABSTRACT: Earth surface processes and landforms may have coadjusted[†] with plant morphology, biomechanics and life-history. We suggest that the colonization of land by plants at the early Silurian, and their propagation inside continents, represent critical phases of the coupling between geomorphic and biological processes on the Earth at a global scale. The consideration of this coupling involving geomorphic-biological feedback mechanisms at the scales of ecological succession and organisms' evolution may promote the emergence of an evolutionary[†] geomorphology. Copyright © 2009 John Wiley & Sons, Ltd.

KEYWORDS: vegetation dynamics; evolution; sediment; landforms; evolutionary[†] geomorphology

Introduction

Since the initial stage of a solidified planet, Earth surface processes and landforms have evolved from strictly abiotic to biotic thermodynamics. Thermodynamics are considered in this commentary from a geomorphic perspective, in terms of mass flux equilibrium (Thorn and Welford, 1994), which encompasses energy and matter flows and cycles of landform construction and destruction. Within abiotic geomorphic contexts, e.g. in hyper-arid or polar regions on the Earth, or on other terrestrial planets such as Mars or Venus, landform dynamics are expressions of a trade-off between the physical and chemical resistance forces defining rocks, sediment and ice cohesiveness, and the mechanical and chemical forces leading to morphogenesis (e.g. gravity, compression, wind or water flow, meteor impacts, dissolution). The appearance and evolution of life on Earth, in particular of plants (for a review see Kenrick and Crane, 1997; Willis and McElwain, 2002), was accompanied by diversions, from very local to the global scale, of energy and matter flow from dynamics related only to the physical and chemical constraints. These diversions encompass an intensification of solar energy capture and storage by plants and through the food web on the Earth surface (Morton, 2007). A part of the energy of net primary production of plants is directly or indirectly converted into geomorphic work (Phillips, in press a), involving mass fluxes and mass storage, i.e. sediment and landform dynamics. In general, the diversions of energy and matter flow from dynamics solely related to the physical and chemical constraints correspond to a global intensification of sediment and organic matter storage on continental zones induced by the increase of sediment cohesiveness and surface roughness by plants (Viles *et al*., 2008).

The consideration of these 'diversions' may lead to the development of a geomorphology which explicitly interlinks physical processes with evolutionary processes. Biological evolutionary processes have recently been incorporated into geomorphology (Stallins, 2006; Corenblit *et al*. 2007a, 2008; Phillips, 2009). In particular, the concept of niche construction (Odling-Smee *et al*., 2003) has been used by the authors to consider feedback mechanisms between Earth surface processes and landforms and living organisms' evolution. The aim of this conceptual commentary, based on results from multidisciplinary scientific literature and thoughtful speculations, is to encourage the geomorphic community to forge a novel way of perceiving Earth surface processes and landforms through the explicit consideration of abiotic–biotic feedbacks at the global scale of the Earth. We focus in this paper on vegetation dynamics as a major evolving geomorphic force. Thus, we intend to contribute to develop the basis of an evolutionary geomorphology.

Vegetation Dynamics: An Evolving Geomorphic Force

Before the appearance of life, in particular plants, three main sources of energy were available to be converted into forces

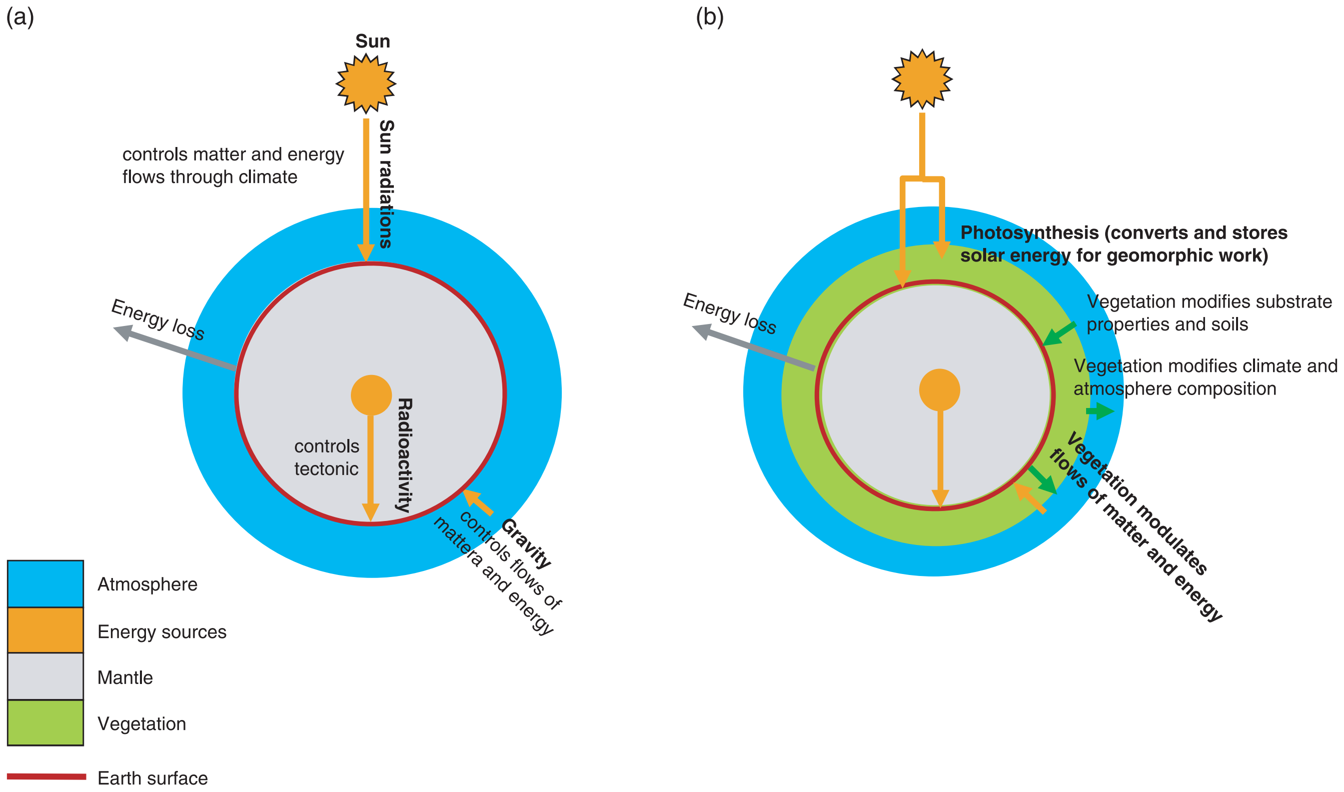

Figure 1. Two simplified models of global geomorphology of the Earth. The Earth as (a) an abiotic geomorphic system controlled by physical and chemical factors; (b) a biotic biogeomorphic system modulated by vegetation dynamics. This figure is available in colour online at www.interscience.wiley.com/journal/espl

producing geomorphic work (Figure 1a). These sources of energy are gravity and solar energy which control exogenous morphogenesis; they are at the origin of sediment erosion, transport and deposition processes on the Earth surface. The third source of energy is endogenic geothermal activity which controls tectonic uplift. In an open dissipative system such as the Earth, tectonics produce heterogeneity in matter and energy distribution leading to a decrease in entropy; and tectonics also increase available kinetic energy for geomorphic work. Gravity and solar energy and their effects on mass transfer and denudation processes tend to homogenize the distribution of matter and energy at a global scale leading to an increase in entropy, thus decreasing the available energy to be converted into geomorphic work.

We argue that vegetation dynamics represent another major geomorphic agent on the Earth surface because it converts solar energy into geomorphic forces with very significant impacts from local to the global scales (Phillips, in press a, 2009) (Figure 1b). One of the fundamental biological processes associated with vegetation dynamics is the photosynthetic conversion of solar radiation into chemical energy. This process is a keystone component of the systemic concept of biosphere represented as a planetary membrane for capturing, storing, and converting solar energy (Vernadsky, 1926). Beyond its primary importance in ecosystem function, photosynthesis represents also a basic important mediator for geomorphic changes with unexpected consequences in terms of geomorphic thermodynamics and evolutionary processes. Photosynthesis led to a shift from abiotic geomorphic toward biotic biogeomorphic dynamics on the Earth. By converting solar energy into carbohydrates and cellulose, photosynthesis permitted plants to perform geomorphic work through their biomechanical and biochemical impacts on rocks, sediment and soil dynamics. These effects are produced by roots which modify substrate texture, structure, cohesion and chemical properties (Viles, 1995; De Baets *et al.*, 2006; Wilkinson and Humphreys, 2006; Phillips and Lorz, 2008), and by the aerial structure which increases surface roughness and modulates flows of matter and energy (Tsujimoto, 1999; Li *et al.*, 2003; Corenblit *et al.*, 2007b). Plant roots and aerial structures produce diverse effects such as bioweathering, bioturbation, bioprotection and bioconstruction which are recognized to act on the long term at large scales (Naylor *et al.*, 2002; Viles *et al.*, 2008). The combination of the direct effects of roots and aerial structures produces at local to regional scales characteristic patterns of landforms (Table I), for example such as parabolic dunes, rounded hillslopes, simplified hydrological networks, island braided or meandering rivers with oxbow lakes, salt marshes and mangroves (for a review see Viles, 1988; Corenblit *et al.*, 2008; Viles *et al.*, 2008). Indirect effects concern mainly local to global modifications of the composition of atmosphere and climate (Kleidon *et al.*, 2000; Beerling and Berner, 2005), which in turn control weathering processes, sediment erosion, transport and deposition. Vegetation also represents the primary, either direct or indirect, source of energy for nearly all organisms (animals and microorganisms) which in many cases also control geomorphic processes through their engineering activities in soils and at the surface of the Earth (Butler, 1995).

Colonization of Land by Plants and Effects on Geomorphology

One of the most relevant differences between the geomorphic forces produced by vegetation dynamics and those produced by tectonics and denudation relates to the biological evolutionary components of plants. Emerged land remained barren for more than 3500 Ma and landform dynamics implicated during this period only physical and chemical interaction. However, prokaryotic and eukaryotic organisms present in the oceans as early as 3500 Ma (Nisbet and Sleep,

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Table I. Landform patterns modulated by vegetation on the Earth surface at diverse scales, noting the geomorphological processes controlled or modified by vegetation

Environment	Type of landform pattern modulated by vegetation	Geomorphological processes controlled or modified by vegetation	Reference
Terrestrial/water interface			
Fluvial corridors	Islands; floodplains; river banks; river channels; vegetated channel bars; oxbow lakes	Sediment erosion (vertical and lateral), transport and deposition by water flow	Corenblit *et al.* (2007b)
Peatlands	Islands; floodplains; river channels; oxbow lakes	Sediment erosion (vertical and lateral), transport and deposition by water flow	Watters and Stanley (2007)
Intertidal marshes	Tidal networks; channels; river banks; tidal flats	Sediment erosion (vertical and lateral), transport and deposition by water flow	Bos *et al.* (2007)
Mangrove shores	Tidal networks; channels; river banks; islands; floodplains; tidal flats	Sediment erosion (vertical and lateral), transport and deposition by water flow	Lee (1999)
Coastal beaches	Sand dunes	Sediment erosion, transport and deposition by wind	Stallins and Parker (2003)
Terrestrial context			
Small to large scale surfaces in arid and semi-arid environments	Sand dunes; hillslopes (e.g. alluvial fans, screes, talus cones)	Sediment erosion, transport and deposition by wind and water flow; rock weathering	Saco *et al.* (2007)
Small to large scale surfaces in tropical and temperate contexts	Hillslopes; hydrographic networks; solifluction lobes	Sediment erosion, transport and deposition by water flow; solifluction; soil creep; rock weathering; rainsplash	Phillips and Lorz (2008)
Small to large scale surfaces in sub-arctic and alpine contexts	Hillslopes; thufurs, solifluction lobes, sorted stripes; nival niches	Sediment erosion, transport and deposition by wind and water flow; frost sorting; freeze–thaw; solifluction; nivation; rock weathering	Kozłowska and Rączkowska (2002)

2001) and 2700 Ma (Brocks *et al.*, 1999), respectively, profoundly impacted geomorphic dynamics of the Earth at regional and global scales even before starting to colonize emerged lands. Some prokaryotic and eukaryotic organisms, including photosynthesizers since 3300 Ma, are considered to be at the origin of plants. Phylogenetic studies suggested that green algae in particular are the ancestor of land plants (Kenrick and Crane, 1997). Cyanobacteria produced large-scale bioconstructions known as stromatolites fossil reef mounds or bioherms (Ramussen, 2000), and by producing oxygen, transformed drastically the atmosphere's composition (Holland, 1984). This transformation has deeply modified weathering and erosion processes on the emerged continents at the global scale and enabled first plants and then animals to colonize emerged lands. Furthermore, before colonization by vascular plants, the bare substrate did not contain biological available elements such as iron (Fe) and phosphorus (P). The organic acids produced in the intertidal zones by the early prokaryotic and eukaryotic organisms, and probably also by lichens (Retallack, 1994a), contributed to rock weathering and soil formation (Retallack, 1985), and thus prepared plant terrestrialization. In this changing context, plants probably evolved from marine plants, moved into freshwater (i.e. ocean margins and fluvial corridors) and finally onto land (Willis and McElwain, 2002). This transition from marine green algae to simple bryophyte type plants to complex vascular plants was accompanied by the evolution of mechanical support structures, anchoring mechanisms and efficient dispersal mechanisms for colonizing land. This shift may have involved joint adjustments of Earth surface processes and landforms according to the evolution of the morphology and biomechanics of aerial plant structures and roots and their effects on sediment dynamics.

Colonization at the early Silurian (470–430 Ma) of land by plants able to protect against desiccation, to uptake water and nutrient, to support mechanically and to anchor in the substrate (e.g. *Cooksonia pertonii*, *Aglaophyton major*, *Rhynia gwynne-vaughanii*, *Zosterophyllum divaricatum*; for a full description see Willis and McElwain, 2002) represent a critical phase for geomorphic changes on the Earth surface. The development of mechanical support at the beginning of this period was linked to structural organization of the plants into large, wide, flat canopy, short and wide semi-rigid stems, outer cortical tissue, and collenchyma (Niklas, 1997). Traces of roots dating around 408 Ma have been found. They indicate the existence of dichotomous roots between 5 and 20 mm in diameter and close to 1 m in length (Elick *et al*., 1998). Such kind of biomechanical solutions developed by plants since the beginning of the Silurian to obtain access to nutrient resources affected weathering processes and erosion/deposition dynamics on the Earth surface. Accelerated weathering by roots has been linked to the formation of Devonian and early Carboniferous (420 to 320 Ma) marine black shales (Algeo *et al*., 1995). Viles *et al.* (2008) point out that, according to Berner and collaborators' hypothesis that vegetation roots accelerated chemical weathering of silicate minerals during the Devonian (Berner, 1993, 1998; Berner and Kothavala, 2001), the development of rooted vegetation and soil systems amplified and thus, contributed to the rapid acceleration of the drawdown of atmospheric carbon dioxide (CO_2) in the Devonian. This decrease in CO_2 concentration favoured the process of plant terrestrialization, and major evolutionary changes in plant structure, shape and reproduction occurred (Willis and McElwain, 2002), potentially inducing enormous impacts on geomorphic processes.

During the Silurian, vegetation corresponded most commonly to small (less than 1 m height) non-vascular or vascular plants. However, many geomorphic and ecological studies (e.g. Friedrichs and Perry, 2001) indicate that comparable plants in terms of size and biomechanics (e.g. salt marsh plants such as *Spartina* spp.) induce very significant fine sediment trapping and protection from erosion, thus producing very characteristic ecosystems and geomorphic patterns in intertidal zones. Vascular plants first clung in the late Ordovician/early Silurian to lowland wetlands such as estuaries and fluvial systems and probably deeply modified soils and landform dynamics associated to these geomorphic systems. The global annual volume of fine sediment storage within Silurian wetlands may be difficult to gauge. However, it is reasonable to state that the global fine sediment transfer from land to ocean at this period probably experienced an increase of mass-storage in the vegetated wetlands.

Colonization of drier lands by plants represents another critical phase for geomorphic changes associated with plant biomechanical innovations to face environmental constraints such as gravity, desiccation, or wind and water flow. These adaptations encompassed life-history traits (e.g. new modes of reproduction through the dispersion of spores and seeds in emerged conditions) but also morphological and biomechanical traits. Between 390 and 365 Ma, complex root and stem systems, woody structures, barks and leaves started to appear. New plant species developed bigger structures and additional supporting mechanisms (e.g. thickening of trunk with wood and bark, extensive underground rooting systems up to 1 m deep; for a review see Willis and McElwain, 2002). According to these authors, all these innovations facilitated large increases in plant size and structure. Global vegetation evolved between the middle Devonian to late Carboniferous (380–290 Ma) from small plants to complex forested ecosystems with diverse stratas (including dead woods) dominated by trees of 30 m in height (e.g. *Lepidodendron*, *Calamites*, *Psaronius*, *Archaeopteris* trees; for a full description see Taylor and Taylor, 1993). Plants could spread efficiently to the inside of continents and could colonize diverse geomorphic systems. Gymnosperms, which were very widespread and now able to grow in dry areas, played a major role in colonizing continents from the beginning of the Permian (290 Ma). The Jurassic (208–145 Ma) was characterized by the dominance of gymnosperms and a widespread distribution of ginkgoales. Angiosperms emerged in the Cretaceous (145–65 Ma) and remain dominant today (Willis and McElwain, 2002). Angiosperms are represented by a large range of morphotypes encompassing, herbaceous, shrubby and arboreous structures and colonized efficiently the Earth's surface.

The evolution of morphological, biomechanical and life-history traits of plants during the last ~440 Ma may have deeply affected the quality, the frequency and the intensity of bioweathering, bioturbation, bioprotection and bioconstruction at a global scale. This hypothesis is supported by the review of Phillips and Lorz (2008) which illustrates the extreme efficiency of plants in modifying substrate properties and geomorphic processes. In particular the development of the lignin-containing plants (shrubs and trees) in the middle Devonian (380 Ma) have produced the most significant geomorphic changes. Their complex and resistant root and stem systems combined with their slower decomposition has contributed to increase global sediment stability and storage in time and in space on the Earth's surface. They also contributed to the formation of soils which have continued to coevolve with biota (Retallack, 1990, 1994b; Phillips and Lorz, 2008).

Thus, plant appearance and evolution may be considered from a geomorphic point of view as major components of the geomorphic history of the Earth. Vegetation has induced continuous and oriented modifications of surface processes from the micro-scale of landforms to the global-scale of sediment budgets from hillslopes to rivers and from rivers to plains and oceans.

Toward an Evolutionary Geomorphology

The perspective presented here points to the possibility that natural selection which accompanied and oriented the emergence and evolution of plants according to Darwin (Darwin, 1859) represents an underlying fundamental biological conductor for physical and chemical changes, including geomorphic components (Figure 2). Geomorphic changes have to be perceived here according to the concept of niche construction (Odling-Smee *et al.*, 2003). Through this perspective, it is suggested that the quality and the intensity of modulations of geomorphic processes and patterns by vegetation dynamics on the Earth surface have changed according to the selection of genes producing engineering (*sensu* Jones *et al.*, 1994) or niche constructing plant biological traits. The engineering biological traits relating to plant morphology, biomechanics and life-history are those that modify significantly directly or indirectly their physical environment including landforms. The niche construction perspective implies that the evolution of vegetation

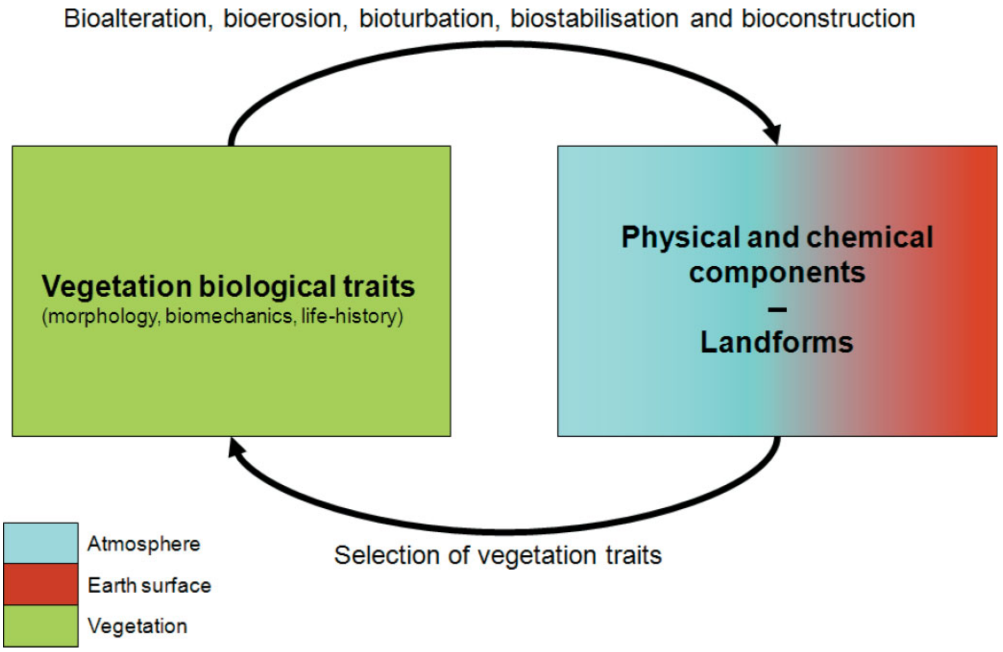

Figure 2. Model of reciprocal interactions and adjustments between vegetation and Earth surface dynamics at evolutionary timescales. This figure is available in colour online at www.interscience.wiley.com/journal/espl

engineering traits is not independent from the modifications they induce to their environment. Feedback mechanisms occur between the environmental changes produced by the engineering organisms and the process of natural selection (Odling-Smee *et al*., 2003). This is illustrated in this commentary by the inter-linkage between plant innovations and global scale changes in the physical compartments (i.e. atmosphere and substrates). From a biogeomorphic point of view, engineering vegetation species and Earth surface processes and landforms co-adjust and co-define on the long term producing characteristic evolving assemblages of landforms and associated communities of living organisms (Corenblit *et al*., 2008).

Dietrich and Perron (2006) suggested that, although living organisms strongly influence the matter and energy fluxes on continents and may have altered profoundly the course of Earth's evolution and its landscapes, it may not be possible to detect a 'unique' (i.e. a landform that could only exist in the presence of life) and characteristic topographic signature of life. Dietrich and Perron expect that topographic signatures of life on Earth are more subtle than the presence of certain diagnostic, i.e. unique, landforms; and that this subtlety is likely to be (i) of frequency of occurrence of certain landform properties and (ii) of scale. Geomorphic signatures of life are complex and of multiple kinds on the Earth's surface and may encompass to a certain extend unique geomorphic patterns and dynamics at various scales according both to autogenic engineering (*sensu* Jones *et al*., 1994) productions such as coral reefs, and allogenic engineering productions such as termite-mounds, anthills, and galleries in soils. In accordance with Dietrich and Perron (2006), geomorphic signatures of life also correspond to subtle modulations of geomorphic components (e.g. geometry, texture, landform turnover) by engineering organisms. This is illustrated for example by sand dunes (Stallins and Parker, 2003) and alluvial bars (Gurnell and Petts, 2006) which exhibit, under the control of vegetation, differences in their geometry and dynamics relative to their abiotic pair in equivalent conditions (Table I). Such a concept of a characteristic biological imprint on geomorphology initiated from Charles Darwin's (1881) observations. In his last scientific book on *The Formation of Vegetable Mounds through the Action of Worms with Observations on their Habits*, Darwin identified a typical geomorphic signature of life in soils associated to bioturbation. This foundation example is not anecdotic since burrowing organisms affect soil formation, erosion and hillslope stability in most of the surface of the Earth (Meysman *et al*., 2006). Phillips (in press b) recently described this kind of biotic signature in soils as an 'Extended Composite Phenotype'.

The theoretical insights enounced in this article imply that the characteristic geomorphic patterns which are stable under the control of certain engineering plant species become unstable under the control of other engineering plant species with particular morphological, biomechanical and life-history traits; and/or when geomorphic disturbance regimes change deeply (Viles *et al*., 2008). Thus, the modulation of geomorphic processes and landforms by vegetation may have fluctuated in quality and intensity in space and in time according to the reciprocal coupling between physical environmental changes and vegetation evolution. This hypothesis suggests that some characteristic patterns of landforms (i.e. shape, texture, resistance to disturbance, time of existence) linked to vegetation dynamics may have evolved and disappeared, in a certain 'envelop' of geomorphic constraints, conjointly with the evolution and extinction of particular keystone or foundation engineering plant species. Furthermore, new types of modulations of landform patterns may develop in the future in association with the evolution of new engineering biological traits.

Such consideration on the evolutionary effects, and responses, of vegetation on Earth surface processes and landforms from local to global scales will contribute to the development of a complementary field of investigation for biogeomorphology which encompasses reciprocal linkages between abiotic and biotic factors. We propose to name this perspective, which extends the effects of natural selection (*sensu* Darwin, 1859), to the geomorphic component of Earth, 'evolutionary geomorphology'. The choice of this term is based on the following considerations. Geomorphic systems exhibit typically non-linear behaviours, including dynamic instability and deterministic chaos (Phillips, 2005, 2006a). Instability indicates divergent evolution (used here in its general sense to mean systematic change over time), increasing differentiation in matter and energy organization over time, and the persistence and growth of disturbance effects and initial variations. Dynamic instability and deterministic chaos imply that evolution of geomorphic systems is generally divergent, sensitive to initial conditions and to small perturbations. Thus, Phillips (2006b) proposed that geomorphic systems are 'evolutionary'. 'Evolutionary geomorphology' (*sensu* Phillips, 2006b) is 'an approach to the study of surface processes and landforms which recognizes multiple possible historical pathways rather than an inexorable progression toward some equilibrium state or along a cyclic pattern' (Phillips, 2006b). Our biogeomorphic approach of Earth surface processes and landforms is based explicitly on the consideration of extended effects of natural selection. It can be considered as complementary to the conceptual model of 'evolutionary geomorphology' by Phillips (2006b) and the recently proposed concept by Viles *et al.* (2008) in which interactions between organisms and geomorphic components of natural systems act as intrinsic feedback factors modulating the response of these systems to matter and energy fluxes and to exogenous physical disturbances.

We consider that vegetation will represent a major component of this field of investigation and we strongly encourage the development of further links between geomorphology, plant ecology and evolutionary biology. The success in clearly demonstrating existing, emerging and evolving biogeomorphic structures (and associated functions at the scale of the ecosystem) will depend on interdisciplinary approaches leading to the identification of the keystone or foundation engineering species and communities which modulate Earth surface processes and landforms in a given area. Field and experimental studies will need to be undertaken to assess in priority the range of variation of the effects and responses of engineering species or communities according to prevailing geomorphic processes.

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