

RESEARCH
REVIEWS



Engineer pioneer plants respond to and affect geomorphic constraints similarly along water–terrestrial interfaces world-wide

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ABSTRACT

Aim Within fluvial and coastal ecosystems world-wide, flows of water, wind and sediment generate a shifting landscape mosaic composed of bare substrate and pioneer and mature vegetation successional stages. Pioneer plant species that colonize these ecosystems at the land–water interface have developed specific traits in response to environmental constraints (response traits) and are able to modify habitat conditions by modulating geomorphic processes (effect traits). Changes in the geomorphic environment under the control of engineer plants often feed back to organism traits (feedback traits), and thereby ecosystem functioning, leading to eco-evolutionary dynamics. Here we explain the joint foundations of fluvial and coastal ecosystems according to feedback between plants and the geomorphic environment.

Location Dynamic fluvial and coastal ecosystems world-wide.

Method Drawing from a pre-existing model of ‘fluvial biogeomorphic succession’, we propose a conceptual framework showing that fluvial and coastal ‘biogeomorphic ecosystems’ are functionally similar due to eco-evolutionary feedbacks between plants and geomorphology.

Results The relationships between plant traits and their geomorphic environments within different fluvial and coastal biogeomorphic ecosystems are identified and classified within a framework of biogeomorphic functional similarity according to three criteria: (1) pioneer plants develop specific responses to the geomorphic environment; (2) engineer plants modulate the geomorphic environment; (3) geomorphic changes under biotic control within biogeomorphic ecosystems feed back to organisms.

Main conclusions The conceptual framework of functional similarity proposed here will improve our capacity to analyse, compare, manage and restore fluvial and coastal biogeomorphic ecosystems world-wide by using the same protocols based on the three criteria and four phases of the biogeomorphic succession model.

Keywords

Biogeomorphic ecosystem, biogeomorphic succession, coastal dune, eco-evolutionary dynamics, ecosystem engineer, mangrove, niche construction, plant trait, river, salt marsh.

INTRODUCTION

The geomorphic heterogeneity and variability of fluvial and coastal ecosystems (i.e. rivers, coastal and estuarine salt marshes and mangroves, coastal dunes) makes them among the most dynamic and productive ecosystems over extensive linear stretches of the Earth's surface. These ecosystems at the interface between land and water (Fig. 1) encompass an enormous diversity of physical configurations, and species life-forms and assemblages, reflecting the regional and local geological, geomorphic and bioclimatic settings. However, they also share common features reflecting the relation between plant dynamics and the geomorphic environment.

The structure and function of any physically disturbed fluvial or coastal ecosystem (e.g. meso- to macrotidal conditions along the coast, piedmont to floodplain river reaches) result from feedbacks between plant dynamics and the motion of water, wind and sediment. Based on the strong feedbacks between plants and geomorphology, Balke *et al.* (2014) recently termed fluvial and coastal ecosystems 'biogeomorphic ecosystems' (BE), implying that ecosystem structure and function (i.e. habitat

properties and species assemblages; matter and energy fluxes) are emergent properties of plant–geomorphic feedbacks. These feedbacks exist because of the ability of plants to adjust their characteristics to a geomorphologically dynamic environment by genotypic or phenotypic adaptation, enhancing connectedness (i.e. the degree to which the integrity of an ecosystem is controlled through internal feedbacks between small- and large-scale processes) and resistance and resilience (i.e. the ability of the system to recover from physical disturbances) (see Holling, 1973). The BEs we define here relate exclusively to 'geomorphologically dynamic ecosystems', which are unstable and subject to frequent and regular physical disturbance. The BE concept is directly related to the 'fluvial biogeomorphic succession' (Corenblit *et al.*, 2007, 2009a), which encompasses four phases of matter and energy organization in space and time (i.e. geomorphic, pioneer, biogeomorphic, ecological; Fig. 2). Each phase is linked to different time- and space-limited ecosystem structures and functions and is characterized by a specific set of interactions and feedbacks between plants and geomorphology.

The *geomorphic phase* is the rejuvenation phase following a flood, storm or tsunami, during which the properties and sta-

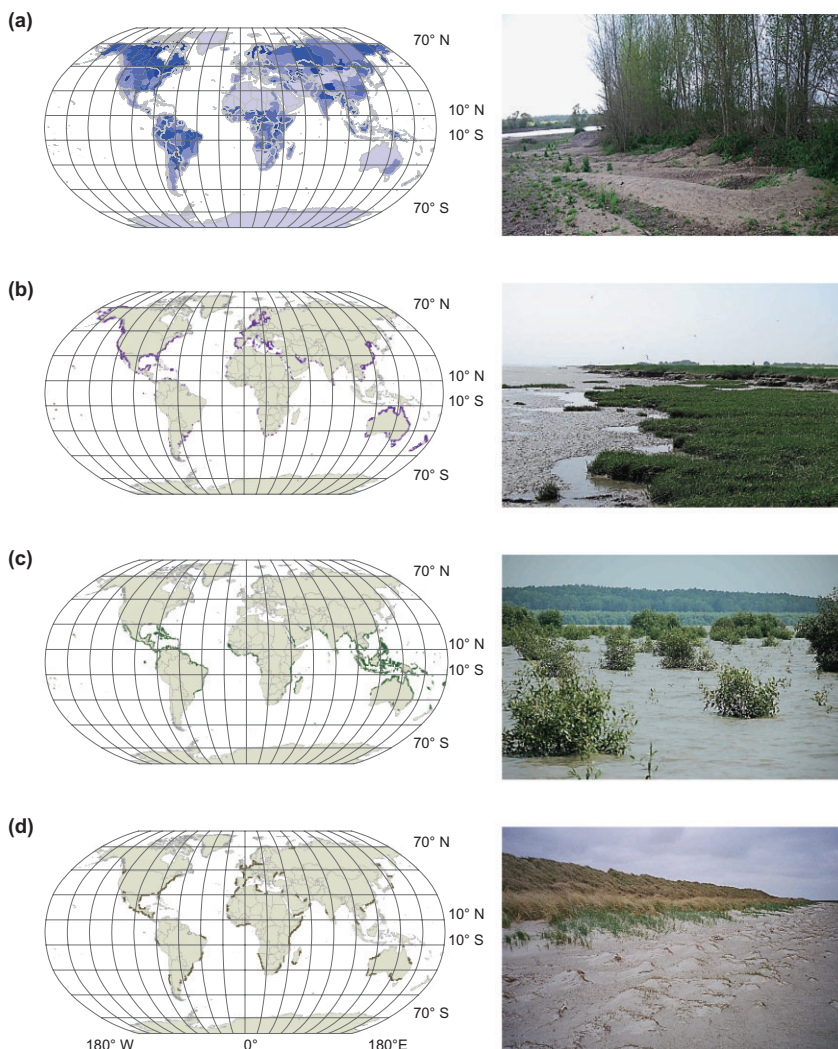


Figure 1 Global distribution of distinct fluvial and coastal biogeomorphic ecosystems (BEs). (a) River abundance by ecoregion defined from low (light shading) to high (dark shading) (Abell *et al.*, 2008; photo J. Steiger). (b) Salt marsh distribution (UNEP WCMC, 2013; photo T. Balke). (c) Mangrove distribution (Giri *et al.*, 2011; photo T. Balke). (d) Coastal dune distribution (Martínez *et al.*, 2004; photo J.A. Stallins).

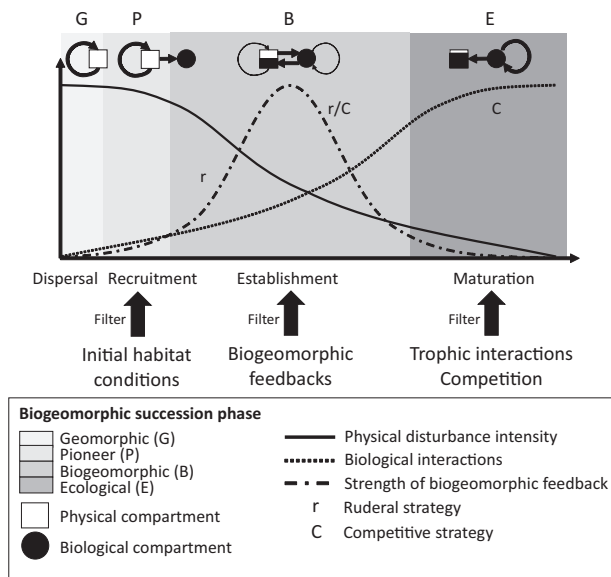


Figure 2 Conceptual model of biogeomorphic succession (*sensu* Corenblit *et al.*, 2007, 2009a). Interactions between the physical (squares) and biological (circles) compartments are shown for each phase (inspired from Odling-Smee *et al.*, 2003). Arrows indicate an interaction with its intensity schematized by the size of the line. The influence of engineer plants on the physical compartment is represented by a dark shade within the squares. Physical changes related to early stages of the biogeomorphic phase correspond to sediment accretion and topographic rise; those associated with late stages of the biogeomorphic phase and to the ecological phase correspond to changes in physicochemical properties of the soil.

bility of landforms are mainly defined by hydrodynamic and aerodynamic forces and the intrinsic cohesiveness of sediment. During this phase, the geomorphic environment controls dispersal of plant diaspores (Fig. 2). During the *pioneer phase*, recruitment of vegetation occurs on newly formed bare sediment surfaces, and the geomorphic environment controls seed germination and seedling survival and growth (Fig. 2). During the *biogeomorphic phase*, feedbacks occur between plant and geomorphic dynamics as the morphological and biomechanical characteristics of plants interact with substrate cohesion and geomorphic flows of matter and energy. In the absence of major physical disturbances, changes in the geomorphic environment under the control of plants, and the resulting feedback on plants, result in the stabilization of the ecosystem during the *ecological phase* in which biotic interactions dominate (Fig. 2).

It has been suggested that the ‘fluvial biogeomorphic succession’ model is relevant to dynamic rivers (Davies & Gibling, 2013; Gurnell, 2014; Bätz *et al.*, 2015), and also coastal (Kim, 2012; Balke *et al.*, 2014) and terrestrial BEs (e.g. lateral moraines; Eichel *et al.*, 2013), implying that it could be a useful common foundation for investigating many geomorphically dynamic ecosystems. However, this wide range of applicability does not imply that the number and intensity of plant–geomorphology feedback interactions are the same in each BE

because: (1) many different taxa and floristic assemblages are observed according to local and regional settings; (2) at the same location, divergent trajectories in plant community assemblages can occur during biogeomorphic succession, reflecting variations in initial biological and physical conditions; (3) the duration and spatial extent of each phase of biogeomorphic succession varies with the disturbance regime; (4) different feedback loops exist between plants and geomorphology and related biogeomorphic stability according to the disturbance regime and plant characteristics.

Although BEs around the world show wide taxonomic differences, comparable constraints can lead to convergent patterns of adaptive *traits* developing across taxa, as implied by the functional framework of adaptive CSR (competitor, stress tolerator, ruderal) strategies proposed by Grime (2001). A ‘trait’ is any morphological, biomechanical, physiological or phenological feature measurable at the individual level, from the cell to the whole organism (Violle *et al.*, 2007). Many pioneer plant species have homologous traits that optimize their capacity for reproduction, survival and growth (i.e. fitness) within areas exposed to water, wind and sediment flows (Hesp, 1991; Bornette *et al.*, 2008). This does not mean that all co-occurring species have the same characteristics; alternative strategies may co-occur to cope with a stress, causing a few response trait-groups to co-inhabit a specific habitat (Stallins, 2005; Puijalón *et al.*, 2011).

We suggest that fluvial and coastal BEs are functionally similar as a result of dominant feedback mechanisms between the geomorphic environment and plant *response, effect and feedback* traits. Here, *response traits* are any plant attributes that provide an adaptive response to water or wind flow, sediment erosion, transportation and deposition, and lead to successful dispersal, recruitment, establishment and reproduction. *Effect traits* are morphological and biomechanical plant traits that induce a significant effect on the geomorphic environment. Within BEs, response and effect traits are strongly linked and may coincide because successful colonization is a prerequisite for plants to affect the geomorphic environment and create biogeomorphic feedbacks. For example, a multi-stemmed flexible morphology may increase the capacity of a plant to resist hydrodynamic forces (response) while also affecting sediment fluxes and topography (effect). We define *feedback traits* as those that provide a response to the modification they induce in the geomorphic dimensions of their niche.

Based on a critical review of ecological and geomorphological investigations of fluvial and coastal ecosystems across the world, we highlight below how different engineer (*sensu* Jones, 2012) pioneer plants respond to wind, water and sediment flows and affect geomorphic processes in a similar way, leading to an enhanced understanding of the role of plant traits in geomorphologically dynamic ecosystems that opens new research perspectives.

The trait-based approach we propose here for defining a BE is founded on three key criteria related to the geomorphic setting and to the nature of its relation with plants (Fig. 3): (1) plants must have developed specific response traits to the geomorphic environment and its disturbances; (2) they must display effect

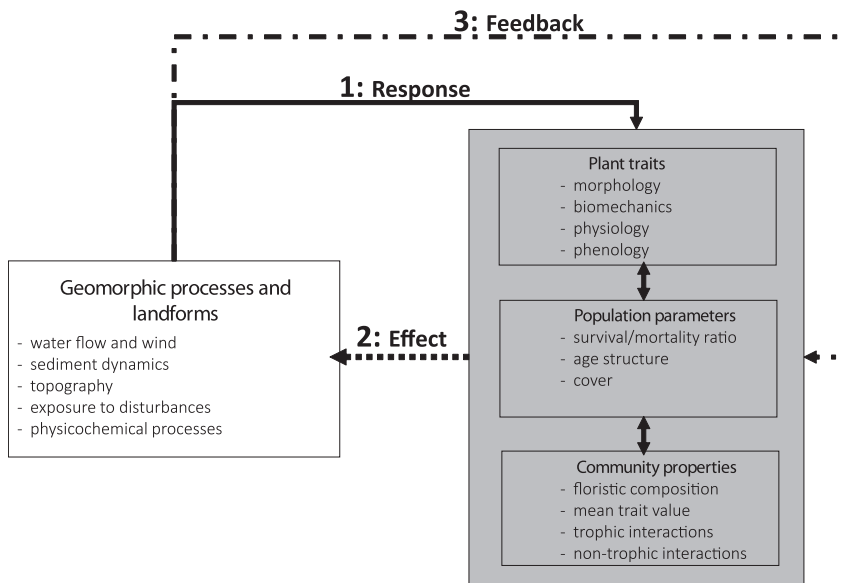


Figure 3 Criteria related to the geomorphic setting and the nature of its relation with plant traits that a certain ecosystem has to satisfy in order to be identified as a biogeomorphic ecosystem (BE). Criterion 1: pioneer plants developed specific responses to the geomorphic environment (response traits). Criterion 2: the geomorphic and physicochemical environment is modulated by engineer plants (effect traits). Criterion 3: geomorphic changes under the control of plants feed back to organisms (feedback traits).

traits that control the geomorphic environment; (3) they must display feedback traits to these biotic-controlled geomorphic changes. In the presence of a biogeomorphic ecosystem *sensu stricto* all three criteria have to apply to the plants. In this paper the term ‘trait’ (response, effect and feedback traits) will be used as recommended by Violle *et al.* (2007) specifically at the level of individuals. However, responses, effects and feedbacks can relate to varying spatio-temporal levels including individuals (i.e. plastic and evolutionary adjustments of traits), populations (i.e. changes in the survival–mortality ratio, age structure, cover) and communities (i.e. adjustments in short- and long-term floristic assemblages and biodiversity).

CRITERION 1: RESPONSE TRAITS OF PIONEER PLANTS TO THE GEOMORPHIC ENVIRONMENT

BEs are unstable and subject to a physical disturbance regime

Most fluvial and coastal BEs consist of unconsolidated sediment and are subject to a natural disturbance regime (i.e. variations in river water flow, tidal currents and waves, or wind), incorporating low- to medium-magnitude variations in hydrodynamic and aerodynamic forces and also less predictable medium- to high-magnitude exceptional fluctuations during extreme events (Naiman *et al.*, 2008). Within rivers, the disturbance regime corresponds to seasonal variations in water level and velocity and medium-intensity flow pulses together with isolated intense flood events. Within salt marshes and mangroves, the disturbance regime corresponds to daily and seasonal or longer variations in tidal water level, ocean waves and isolated storm or tsunami events (Walcker *et al.*, 2015). Within coastal dunes, it relates to seasonal variations in extratropical and tropical storm tracks, mean wind velocity and direction, and isolated storm and tsunami events (Balke *et al.*, 2014).

Plant assemblages and their corresponding functional structure within BEs vary along gradients of exposure to these physical disturbances (Fig. 4), and also along gradients of stress related to anoxia, salinity, drought or competition. Within fluvial ecosystems these gradients are superimposed onto transverse gradients of hydrogeomorphic connectivity and topography from the channel to the floodplain (Bornette *et al.*, 2008; Fig. 4a). Within salt marshes and mangroves they are superimposed onto gradients of wave energy, the influence of tides, micro-topography and salinity from the seashore to inland (Thom, 1967; Fig. 4b,c). Within coastal dunes they are superimposed onto gradients of exposure to aerodynamic and hydrodynamic forces, topography and salinity from the shoreline to inland (Stallins & Parker, 2003; Hesp & Martínez, 2008; Kim & Yu, 2009; Fig. 4d).

The disturbance regime acts as an environmental filter of response traits

At the earlier stages of biogeomorphic succession, and in comparison with biological disturbances such as grazing and bioturbation by animals, the disturbance regime represents the pre-eminent selection pressure for riparian and coastal plants (1 in Fig. 3). It acts as a strong environmental filter of response traits throughout the biogeomorphic succession (Fig. 2; Table 1). Response traits of engineer plants adapt over the long term to the most regular component of the physical disturbance regime (Lytle & Poff, 2004; Naiman *et al.*, 2008). At the establishment stage, selection among the pool of species reflects response traits that favour high net productivity, dispersal, reproduction and survival rates. Many pioneer riparian and coastal species share equivalent response traits (e.g. sexual/vegetative reproduction; body and seed size) related to their morphology, physiology and phenology (Table 1). Optimization of plant traits to water, wind and sediment flows does not necessarily result in convergence, but it may cause divergence of

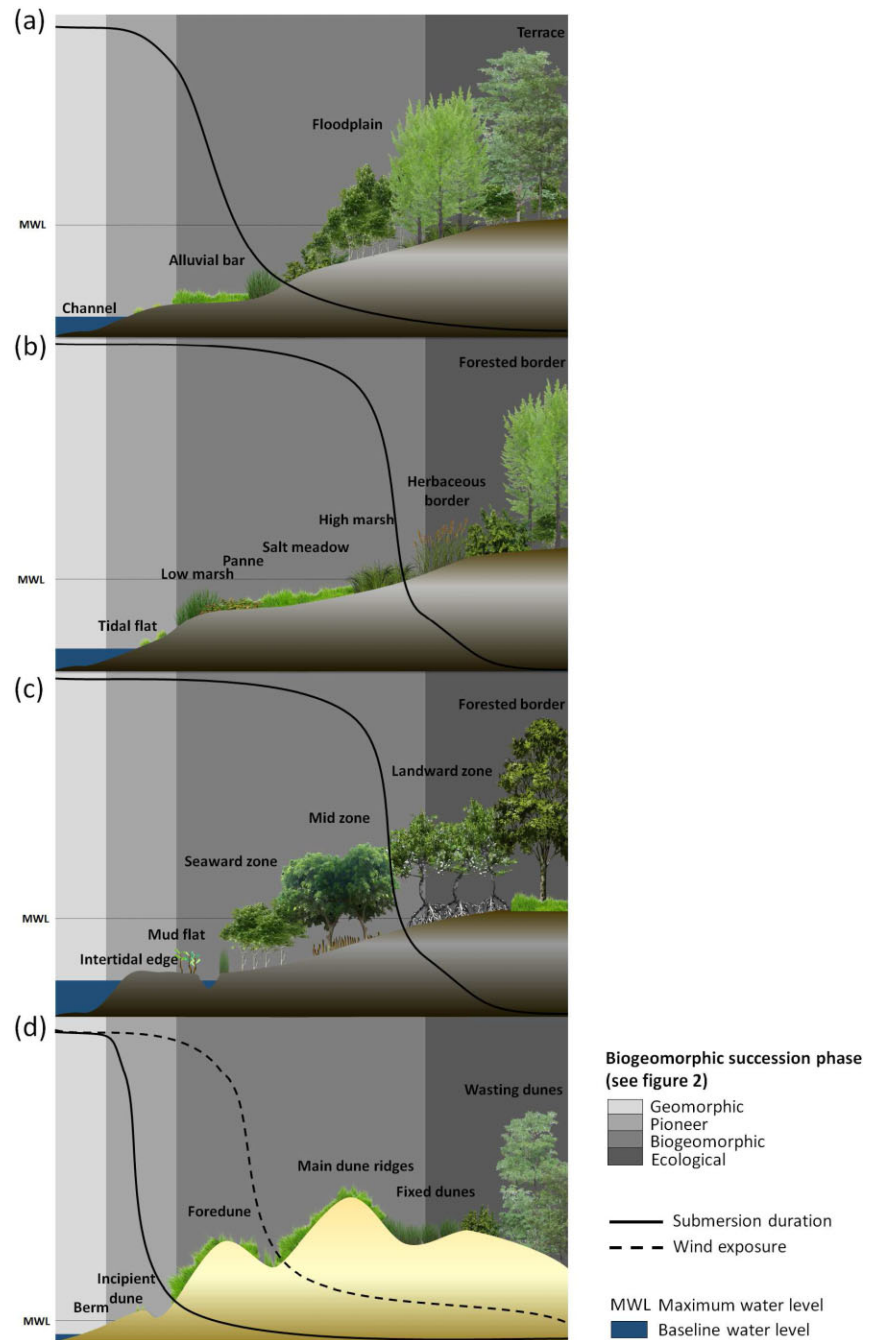


Figure 4 Exposure gradients to hydrogeomorphic and aerodynamic disturbances in fluvial and coastal biogeomorphic ecosystems (BEs). Hydrogeomorphic disturbance is represented in terms of water level variations for all the ecosystems and has different impacts depending on the specific biogeomorphic succession phase (represented in the line at the bottom of each ecosystem).

traits based on the disturbance regime, resulting in contrasts in the way pioneer plants and flows interact and modulate geomorphic processes and landforms (Bouma *et al.*, 2005, 2013; Stallins, 2005).

Pioneer plants can respond to physical disturbances and sustain viable populations through resistance and resilience mechanisms (Table 1), where resistance is the capacity of the plant to maintain its structure or biomass during disturbances and resilience is the capacity of the plant to restore its structure or biomass after disturbances. In many cases high-frequency disturbances of low to medium intensity are essential for the

expression of response traits favouring plant resistance and resilience within fluvial and coastal BEs.

Plant response traits during the geomorphic phase

During the geomorphic phase, the geomorphic environment controls the biotic compartment (Fig. 2), especially diaspore dispersal, which is a crucial process that may coincide with predictable (seasonal) hydrogeomorphic or aerodynamic conditions that guarantee successful recruitment. Recruitment of pioneer populations in BEs requires diaspore release to occur at

Table 1 Developmental sequence of biogeomorphic ecosystems (BEs) during the biogeomorphic succession and related plant functional traits. The functional structure of a BE is shaped by a set of plant species specifically adapted to geomorphic disturbances and to stress. Such species are related, for example within temperate fluvial BEs, to the genera *Alnus*, *Populus*, *Salix* and *Tamarix*; within tropical mangrove BEs to *Avicennia*, *Ceriops*, *Rizophora* and *Sonneratia*; within temperate salt marsh BEs to *Juncus*, *Puccinellia* and *Spartina*; and within temperate dune BEs to *Ammophila*, *Cakile*, *Panicum* and *Urtica*. Many species of these genera developed similar functional traits specifically related to regular and ordinary variations in hydrodynamic and aerodynamic forces and also to a certain range of energy pulses and their subsequent consequences for sediment erosion, transportation and deposition. Here, the common and specific functional traits of the four different BEs are listed and related to each biogeomorphic succession (BS) phase.

Biogeomorphic succession phase	Duration of the BS phase	Main characteristics	Main geomorphic processes and landform formation	Main ecological processes	Common and specific plant functional traits
Geomorphic	Continuous at a local scale within certain locations (e.g. entrenched channels); enhanced by high-frequency disturbances (e.g. formation of convex bar during progressive meander migration in rivers) and tides within dynamic coastal zones Punctual at larger scales; driven by low-frequency floods and storms or tsunamis	Biogeomorphic rejuvenation and bare surface formation; BE structured mainly by geomorphic processes	Fluvial BEs: landform erosion and alluvial bar formation Salt marsh and mangrove BEs: landform erosion and tidal mudflat deposition Coastal dune BEs: beach/dune erosion and beach accretion	Diaspore dispersal; diaspore and organic matter deposition on open bare sediments	Common: short life span; production of numerous buoyant seeds and propagules; seed release synchronized with the flow regime Salt marsh and mangrove BEs: vivipary and floating diaspores (longer life span in salty water)
Pioneer	Few days to a few months	Establishment of bare surfaces. Geomorphic processes exert a strong and unidirectional control on plants, filtering community composition	Fluvial BEs: alluvial bar formation Salt marsh and mangrove BEs: tidal mudflat formation Coastal dune BEs: beach accretion	Recruitment Germination and sprouting on open bare sediments seedling/resprout	Common: rapid root anchoring; clonal growth from drifting debris and propagules; tolerance of seedlings to submersion and sediment burial
Biogeomorphic	Few years to a few decades	Population establishment; engineer plants control geomorphology and respond to changes in geomorphic environment; overall strong feedbacks between biota and the physical environment	Common: sediment accretion within and downstream/downwind vegetation patches Fluvial BEs: pioneer vegetated islands and benches Salt marsh BEs: tussocks, hummocks, vegetated tidal mudflat Mangrove BEs: vegetated tidal mudflat Coastal dune BEs: coppice dunes, hummocks, foredune, parabolic dune	Dominance of engineer plants; facilitation for some other taxa; taxa exclusion; resource grab uptake in a more and more stabilizing habitat	Common: high growth rate; rapid underwater shoot extension; tolerance to sediment burial and prolonged submersion; control of aboveground and belowground biomass allocation; changes in stem and root morphology and physiology in sediment deposit; shallow rooting; stem buoyancy Fluvial BEs: allocation to belowground biomass and branch sacrifice during the dry season; adaptation to hydrodynamic forces: high bending stability, flexible stems, narrow leaf shape, multi-stemmed resprouting from roots and shoots; brittle twig bases Salt marsh BEs: aerenchyma tissue for transferring oxygen from the atmosphere to submerged roots; tolerance to salt; succulence improving water retention, salt exclusion at the roots; salt excretion with glands Mangrove BEs: adaptations to long submersion in salty water: aerenchyma tissue for transferring oxygen from the atmosphere to submerged roots; pneumatophores; salt excretion and exclusion; salt sequestration into horizontal roots, prop and stilt roots, kneed roots Coastal dune BEs: anatomical adaptation to sediment abrasion
Ecological	Few decades to a few centuries	Older ecological succession (post-pioneer to mature stabilized stands); BE dominantly structured by biotic interactions	Fluvial BEs: vegetated floodplains and mature islands Salt marsh BEs: raised vegetated tidal mudflat Mangrove BEs: raised vegetated tidal mudflat Coastal dune BEs: stabilized parabolic and plain vegetated dunes	Plant succession Increase of biotic interaction (e.g. competition and positive interactions such as symbiosis) Pedogenesis	Common: development of competitive traits (e.g. large size) to access resources more efficiently and reproduce in a stabilized environment

the same time as adequate abiotic conditions. Phenological response traits of many plant species are intimately coupled to the periodicity and intensity of hydrogeomorphic constraints (Bornette *et al.*, 2008; Maun, 2009; Balke, 2013; Table 1). In order to cope with the inherently stochastic nature of the geomorphic phase, pioneer engineer plants generally employ opportunistic strategies (*sensu* Grime, 2001; Table 1). Diaspores are mostly produced in very large numbers and can remain viable for a long period. Their production and release are usually well synchronized with the disturbance regime and climate patterns. For example, within temperate river environments seed production and release by riparian *Populus* and *Salix* species coincides with the period following predictable annual floods (Lytle & Poff, 2004; Stella *et al.*, 2006) so that their small, buoyant seeds are transported by water and wind to newly formed bare sediment surfaces. In coastal environments, diaspores (seeds, rhizomes, stolons, roots and branches) are mainly hydrochorous (Table 1). They are mobilized and transported by water, usually during floods and storms (Maun, 2009), and they maintain their capacity to germinate and sprout after transportation in salty water (Guja *et al.*, 2010). Within mangroves formed by *Rhizophora* and *Avicennia* species, massive propagule production occurs during the wet season when salinity is low (Fernandes, 1999). Within coastal dune BEs, certain annual species release large quantities of seeds during the period having the highest availability of the bare moist coastal substrates required for seed germination (Wagner, 1964).

Plant response traits during the pioneer phase

The transition toward more vegetated states that accompanies amelioration of the harsh abiotic environment is highly variable because initial habitat conditions strongly affect initial plant establishment, and the transition requires adequate physical conditions related to combinations of morphological, biomechanical and physiological response traits (Table 1) as well as proximity to a diaspore source or dispersal pathway. In rivers (Cooper *et al.*, 2003), salt marshes and mangroves (Balke *et al.*, 2014), dynamic interactions between numerous fluctuating climatic and geomorphological parameters lead to multiple possible pathways of seedling recruitment on bare surfaces that are only colonized in sufficient numbers every few years. Recruitment success can change with quite small variations in hydrogeomorphic parameters. Similarly, in dune settings, seedling recruitment depends upon the contrasts in wave energy under winter and summer wave regimes and the net balance between seasonal patterns of sediment erosion and deposition, with subsidies from seaweed and other organic wrack debris enhancing the likelihood of seedling recruitment (Davidson-Arnott & Law, 1990).

Once seeds and propagules (e.g. rhizomes, stolons, roots) of pioneer engineer species reach a freshly exposed, bare surface they germinate or anchor almost immediately, whether on alluvial bars within fluvial BEs (Gom & Rood, 1999), on mud flats within mangroves (Guja *et al.*, 2010) or on the upper beach within coastal dune BEs (Maun, 2009). Many riparian (e.g.

Populus and *Salix* species), salt marsh (e.g. *Spartina* and *Puccinellia* species) and mangrove tree (*Sonneratia* and *Avicennia* species) species are highly clonal. The ability to easily resprout is a major advantage for the colonization of areas that are heavily disturbed by extreme events.

During the early stage of the biogeomorphic succession, emerging seedlings or sprouts remain highly exposed to fluctuating hydrodynamic and aerodynamic forces, sediment dynamics and substrate moisture (Mahoney & Rood, 1998; Bouma *et al.*, 2009; Balke *et al.*, 2014). Following germination, rooting anchorage may develop very quickly ensuring strong, early mechanical and physiological resistance to hydrodynamic or aerodynamic forces, sediment burial or stress induced by fluctuations in ground and soil water (Westelaken & Maun, 1985; Guillouy *et al.*, 2011). For example, many viviparous propagules of mangrove trees have pre-formed roots that ensure almost immediate anchoring, and morphological plasticity is already important. Balke *et al.* (2013) showed that sediment burial increases shoot growth and erosion increases root growth of mangrove tree seedlings, increasing their chances of survival according to the disturbance regime. Seedling growth rate is also crucial. Balke *et al.* (2014) identified two conditions for successful recruitment within fluvial and coastal BEs: (1) the coincidence of dispersal events with sufficient hydrodynamic or aerodynamic force to bring an adequate number of diaspores to suitable sites; (2) a sufficiently long period for seedlings to germinate and establish that is free of destructive disturbances. This window of opportunity can last a few days to a few months in fluvial BEs and a few hours to a few days within salt marshes, mangroves and coastal dunes (Balke *et al.*, 2014). Therefore, colonization events can potentially be predicted when information about plant response traits relevant to germination, root growth and plant stability is linked to environmental variables such as water level, wind speed and salinity.

Plant response traits during the biogeomorphic phase

Plants that are adapted to unstable and fluctuating geomorphic environments have high phenotypic variability and plasticity, including modulation of the allocation of above- and belowground biomass, architecture and the biomechanical and physiological properties of organs, features which ensure their resistance to water flow and wind, sediment erosion, burial and sand abrasion (Bornette *et al.*, 2008; Maun, 2009; Table 1). Trait changes result from trade-offs between the need to resist abrasive and tractive mechanical forces, prolonged submersion, and sediment erosion and burial; the need to acquire resources; and the need to adapt the reproductive strategy (clonal versus sexual) to disperse and establish efficiently.

Response traits that support resistance to mechanical constraints are mainly morphological and biomechanical, including: strengthening tissues, stiff stems, prop, stilt and kneed roots, small and streamlined leaves and canopies, and brittle stems with breaking points (Bouma *et al.*, 2005; Bornette *et al.*, 2008; Maun, 2009; Table 1). Pioneer plants are highly resilient to

damage. For example, they can resprout from damaged stumps and rhizomes (Nzunda *et al.*, 2007; Moggridge & Gurnell, 2009) or they can show a plastic morphological and biomechanical response (i.e. thigmomorphogenesis) to repetitive mechanical forces from water or wind, increasing their resistance to breakage and uprooting. Variations in response traits can express a trade-off between tolerance (e.g. a large stem cross-section, production of strengthening tissues, increase in root biomass) and avoidance (e.g. increase in stem flexibility, aerial biomass reduction, morphological reconfiguration of the canopy within water flow and in the wind) (Puijalon *et al.*, 2011), and can have major consequences for a plant's ability to fit to disturbance (Bouma *et al.*, 2005; Stallins, 2005; Gurnell, 2014). When major disturbances are absent, the biogeomorphic phase can be followed by the ecological phase where biotic interactions (e.g. competition) are dominant and physical disturbances rare.

CRITERION 2: EFFECT TRAITS OF ENGINEER PLANTS THAT MODULATE THE GEOMORPHIC ENVIRONMENT

Within BEs, the control of ecosystem structure and function by engineer plants is achieved via durable modification of the habitat (2 in Fig. 3). Three main types of effects of engineer plants on their geomorphic environment can be identified and are explored further below: (1) increase in sediment retention and cohesiveness; (2) divergence of fluid stress; and (3) physicochemical modification and biogenic accumulation.

Increase in sediment retention and cohesion

In fluvial and coastal BEs, the roots and rhizomes of plants increase sediment cohesiveness (Polvi *et al.*, 2014), offering protection against erosion, particularly where pioneer plants have dense root systems and flexible, flattening or creeping canopies. A very well-developed literature demonstrates how such engineer plants obstruct water and wind flows, reducing shear stresses at the ground surface and trapping matter 'within-site' (within their canopy) and 'off-site' (downstream or downwind of the vegetation stand). Within-site effects on sediment trapping and the extent of downstream or downwind deposition vary with canopy structure, fluid properties and sediment transport (Bouma *et al.*, 2013; Nardin & Edmonds, 2014). Individual woody plants or isolated herbaceous patches have a local impact on sediment transport, forming small hummocks or coppice dunes. Isolated groups of dense ligneous and herbaceous perennials form pioneer islands and discontinuous benches at the margins of river channels (Gurnell *et al.*, 2012), large hummocks within salt marshes (Bouma *et al.*, 2009), islands and platforms within mangroves (Fromard *et al.*, 2003) and large coppice dunes, incipient foredunes or parabolic dunes within coastal dune systems (Baas, 2007; Hesp & Martínez, 2008). At larger spatial and temporal scales, between catastrophic floods, storms and tsunamis, engineer plants interact with sediment transport to create large stabilized vegetated islands and floodplains in fluvial BEs, and plain dunes and inter-tidal stabilized

flats in coastal BEs. Pioneer biogeomorphic units also induce off-site effects by protecting downstream and downwind areas and allowing further recruitment. This is illustrated, for example, by the way in which pioneer islands colonized by *Populus nigra* and *Salix* spp. within the high-energy Tagliamento river (northern Italy) enhance the survival of seedling and saplings in sheltered areas (Moggridge & Gurnell, 2009).

Topographic changes induced by engineer plants can reflect species-specific morphology, biomechanics and growth patterns, as illustrated by experiments with tamarisk (*Tamarix* spp.) and cottonwood (*Populus fremontii*) disposed within a mobile sand-bed flume (Manners *et al.*, 2015), where the shrubby morphology of tamarisk resulted in greater reductions in near-bed velocities and sediment flux rates. In another flume experiment the spatial pattern of salt marsh sediment erosion and deposition was observed to vary with morphological and biomechanical effect traits and growth patterns of *Spartina anglica*, *Puccinellia maritima* and *Salicornia procumbens* (Bouma *et al.*, 2013). Furthermore, Perry & Berkeley (2009) showed that the planting of *Rhizophora mucronata* in south-west Indian Ocean mangroves led to structural changes, particularly an increase in fine sediment and organic matter in the intertidal substrate. Krauss *et al.* (2003) found that accretion rates of fine sediment varied with root morphology in Micronesian mangrove forests, particularly with the prop roots of *Rhizophora* spp., root knees of *Bruguiera gymnorrhiza* and pneumatophores of *Sonneratia alba*. Lastly, in coastal dunes of the US Pacific Northwest, Zarnetske *et al.* (2012) observed that dune shape varied with the ability of certain species (*Elymus mollis*, *Ammophila arenaria* and *Ammophila breviligulata*) to trap sand and their growth habit in response to sand deposition (see also Maun, 2009; Pelletier *et al.*, 2009).

Fluid stress divergence

Resistant engineer plants also induce turbulent scouring in their surroundings. Such stress divergence plays a major role in increasing the complexity and diversity of landscapes and forming newly exposed bare substrate locally during the biogeomorphic phase. Pioneer trees that establish on river gravel bars induce sediment scour upstream and laterally (Gurnell *et al.*, 2005). Within coastal BEs colonized by vegetation, entrenched channels are formed through erosion between laterally expanding and aggregating tussocks and vegetated levees (Temmerman *et al.*, 2007). D'Alpaos *et al.* (2007) noted that vegetation controls the formation and geometry of tidal drainage networks according to the combined effects of within-site sediment binding and off-site flow diversion and concentration by plants. Furthermore, dune topography, controlled in part by dune-building plants, can also redirect future overwash and shape local patterns of erosion as well as accretion (Davidson-Arnott & Law, 1990).

The combination of local and downstream or downwind protective–accretive and off-site erosive effects of plants controls spatial and temporal self-organization of BEs, mainly during the biogeomorphic phase (Temmerman *et al.*, 2007; Bouma *et al.*,

2009, 2013; Kim, 2012; Corenblit *et al.*, 2015). It has been further suggested that the pattern of sediment trapping and erosion corresponds to a biogeomorphic scale-dependent feedback. Such feedbacks occur within ecosystems when the landform pattern is reinforced and maintained by a positive feedback in resource acquisition at the local scale (within-site) and when an inhibiting feedback occurs at a larger scale (off-site, at the margins). Evidence for the landscape consequences of scale-dependent feedbacks in BEs is especially strong for rivers (Gurnell, 2014) and salt marshes (Temmerman *et al.*, 2007; Bouma *et al.*, 2009, 2013), although biogeomorphic self-organization also occurs within sand-dune systems (Baas, 2007).

Physicochemical modification and biogenic accumulation

Plants induce physicochemical modification of the habitat and biogenic accumulation within BEs. Such engineer effects in different fluvial and coastal BEs enhance local biochemical activity, improving ecosystem processes and ambient conditions within engineered sites.

For example, in high-energy rivers, Bätz *et al.* (2015) showed how input of organic matter within stabilized pioneer landforms enhances the transition from landforms dominated by fresh sediment deposits towards soil-covered biogeomorphic units such as floodplains. Within salt marshes and mangroves, where the tidal range and the minerogenic sediment input are limited, engineer plants alter the topography through the formation of a peat-like substrate. Morris *et al.* (2002) suggested that coastal engineer plants can control their relative elevation through biomass modulation in order to keep up with sea level rise. Several studies have also shown that many salt marshes and mangroves are able to maintain their surface elevation within the inter-tidal zone over long periods of sea level rise through the modulation of production of root and aerial biomass by plants, and associated peat formation and vertical land-building (Larsen & Harvey, 2010; Marani *et al.*, 2013). Furthermore, fixed dune systems are characterized by the existence of soil catenas that reflect feedbacks between sediment characteristics, topography, drainage conditions and vegetation (Maun, 2009).

CRITERION 3: FEEDBACK TRAITS ASSOCIATED WITH BIOTIC-CONTROLLED GEOMORPHIC CHANGES

Geomorphic changes that occur under biotic control during the biogeomorphic phase feed back into the ecosystem at varying levels (i.e. individual, population and community; 3 in Fig. 3). Changes in individual traits, population parameters and community properties are not just a passive response to initial habitat conditions. During succession, pioneer engineer plants, by controlling landform construction, affect gradients of strategies, population and community dynamics within BEs.

Individual and population-level plant responses to enhanced sediment accretion

Many pioneer engineer plant species that establish within fluvial and coastal BEs require burial by sediment to enhance their anchorage, to favour more vigorous growth and to increase their chances of reaching sexual maturity (Maun, 2009; Corenblit *et al.*, 2014). One or more individual plants that initiate formation of an embryo fluvial or coastal island, a small shadow dune or a tussock can exploit the freshly deposited sediment by developing adventitious roots and rhizomes to stabilize a viable population in a geomorphologically unstable environment (Maun, 2009; Rood *et al.*, 2011) and lead at the micro- to meso-scales to a positive feedback of landform construction, vegetation growth (i.e. feedback traits) and population demographic stabilization. This is exemplified by *Populus* and *Salix* spp. within river environments (Corenblit *et al.*, 2014; Gurnell, 2014), subspecies of *Spartina patens* within salt marshes (Wolner *et al.*, 2013) and *Avicennia germinans* in mangroves (Fromard *et al.*, 2003). This is also well exemplified in coastal dunes by grass species. For example, Zarnetske *et al.* (2012) noted that aerial growth of pioneer engineer plants is favoured by the sediment deposition they enhance in coastal dunes of the US Pacific Northwest. Vertical canopy growth was observed to be stimulated within a few weeks following burial, and the dune-building capacity of engineer species was linked to a specific biogeomorphic feedback between plant growth and architecture, and sediment deposition.

Through spatially explicit feedbacks between vegetation and topography, the diversity of plant traits can canalize patterns of plant establishment and persistence in BEs and lead to different biogeomorphic domains of stability (Stallins, 2005; Corenblit *et al.*, 2009a; Wolner *et al.*, 2013; Vinent & Moore, 2015). For example, in coastal dunes where overwash forcing is more frequent, plants displaying horizontal growth in response to sediment burial (i.e. 'burial-tolerant stabilizers') are reinforced because they enhance a flat topography with low resistance that promotes the likelihood of overwash. Where overwash disturbance is less frequent, plants with vertical growth are favoured by sediment burial (i.e. 'landform builders') since they promote positive-relief topographies. *Ammophila arenaria* produces dense vertical tillers when buried, which favour its development and the development of tall narrow foredunes, while the less dense lateral growth of *A. breviligulata* builds shorter but wider foredunes.

Response of the plant community to geomorphic changes

Sediment accretion and related topographic aggradation under the control of engineer plants also control plant assemblages at the community level through the exclusion of species by burial, the decrease of exposure to disturbance and vegetation shading (Corenblit *et al.*, 2014, 2015). Within rivers and coastal BEs it is the combination of sediment accretion, topographic rise and

vegetation growth that leads to the main changes in the physicochemical properties of the habitat and in floristic assemblages during the biogeomorphic phase (Tabacchi *et al.*, 2000; Gurnell, 2014). For example, when foredunes develop within coastal dunes they reduce the amount of sand and salt spray transported inland, facilitating the incursion of woody vegetation in their protected lees. At the same time, as control by physical constraints diminishes, biogeochemical controls become prominent, with the accumulation of organic matter and shifts in habitat diversity from horizontal (within the habitat mosaic) to vertical (soil to canopy) development (Bätz *et al.*, 2015).

Eco-evolutionary feedbacks

Engineer species certainly change selection pressures within the environment (Wright *et al.*, 2012). Key parameters of the physical environment within BEs are strongly controlled by the effect traits displayed by pioneer engineer plants. We suggest that the long-term history of adaptive changes related to ecological and evolutionary feedbacks between organism response, effect and feedback traits and geomorphic dimensions lead to the emergence of BEs as self-organized adaptive ecosystems *sensu* Holling (1973).

Therefore, the geomorphic gradients and associated community assembly rules and functional structure that are observed within fluvial and coastal BEs need to be considered as emergent properties of short-term (ecological) and long-term (eco-evolutionary) top-down and bottom-up abiotic–biotic feedbacks (Corenblit *et al.*, 2015). Recent palaeontological studies (e.g. Davies & Gibling, 2013) have shown that the evolutionary trajectory of engineer plant traits and many other passenger taxa (microorganisms, fauna and flora) has been modulated over the long term within fluvial BEs by the niche-constructing activity of engineer plants and the resulting network of diffuse co-evolution among the different taxa (Corenblit *et al.*, 2014, 2015). Consequently, eco-evolutionary (*sensu* Erwin, 2008) concepts such as niche construction (Odling-Smee *et al.*, 2003) certainly represent a useful framework for analysing feedbacks between organisms and geomorphology within fluvial and coastal BEs.

FUTURE RESEARCH TASKS

The proposed model of biogeomorphic functional similarity of plant response, effect and feedback traits has the potential to become an operational framework for the articulation of future research priorities of freshwater–terrestrial and saltwater–terrestrial interface systems. This global model of biogeomorphic ecosystem (BE) functioning is also conceived to contribute to the improvement of management and restoration strategies. In order to achieve these goals, we list below future tasks to be investigated for each of the three criteria that define BEs.

Criterion 1: defining the window of opportunity of engineer species

The habitat conditions leading to successful germination and growth of key engineer species must be quantified *in situ*. The quantification of the factors affecting recruitment of plants within fluvial and coastal environments began a long time ago. The ‘recruitment box’ model for fluvial systems of Mahoney & Rood (1998) and the homologous model of a ‘window of opportunity’ for all four BEs proposed by Balke *et al.* (2014) emerged from previous studies. They are both useful operational conceptual frameworks for analysing the relationship between environmental variability and vegetation recruitment during the pioneer phase of the biogeomorphic succession. The hierarchy of the same local and regional factors affecting plant dispersal, germination, initial growth and survival in different locations around the world must be established. Response traits that provide an advantage must be identified and quantified simultaneously *in situ* and *ex situ* in controlled conditions to isolate the key factors (e.g. Guilloy *et al.*, 2011; Balke *et al.*, 2014). Quantitative comparison between different BEs will lead to a formal definition of the world-wide envelope of environmental conditions leading to successful recruitment of engineer plant species that can modulate their geomorphic environment. The frequency histogram of the number (and related functional status) of recruited engineer species along geomorphic niche dimensions, such as for example the mean duration and frequency of disturbances, will be a useful tool for identifying functional groups of responses to geomorphic constraints.

It is also necessary to quantify thresholds of resistance of colonizing engineer plants to the mechanical and physiological constraints imposed by water and wind within BEs. This remains challenging because of dynamic interactions between the fluid, the sediment and the plant (Corenblit *et al.*, 2007) and because of the high phenotypic variability and plasticity of plants. Quantifying these thresholds will also require *ex situ* flume experiments using key engineer species.

Criterion 2: linking plant traits and landform properties

Establishing quantitative understanding of the relation between responses of engineer plants, effect and feedback traits, and landform geometry, dynamics and physicochemical properties is also a priority. Effects of engineer plants on geomorphology must be quantified by considering causal linkages with resulting feedback traits. We consider that the geometrical and physicochemical properties of each category of small- to large-scale coastal and fluvial landforms (e.g. pioneer fluvial or mangrove islands, hummocks, coppice dunes and foredunes) are modulated across the world by the same basic processes but according to specific traits of the local pioneer engineer plant species. The landforms that develop under the control of engineer plants thus exhibit a large range of possible deviations in size, shape, texture, physicochemical characteristics, resistance and resilience relative to their theoretical physical state. Such

deviations are likely to be biologically functional for the engineer species and potentially for passenger species. Therefore, it is an important goal to test the hypothesis of engineered landform functionality at the global scale (Corenblit *et al.*, 2015). This will be achieved by analysing correlations between plant growth performance and type of reproduction, and the frequency histogram of landform properties such as relative elevation, exposure to disturbances (Bertoldi *et al.*, 2011) and physicochemical properties (Bätz *et al.*, 2015). Ultimately, the correspondence between genetic variability of engineer plant species and landform properties must be analysed to establish a genetic basis for the variation of landform geometry and dynamics.

Another important research objective related to Criterion 2 is to test the effects of plant trait diversity on the function of landform construction and ecosystem stabilization. Plant functional traits enhancing sediment cohesiveness and trapping often combine at the community level and form functional units with varying capacities for sediment stabilization and trapping (Corenblit *et al.*, 2009b). Population thresholds of sediment stabilization and trapping might be overridden by the combination of different traits at the community scale. The combination of varying traits, and thus varying genomes, is likely to increase the stability of the biogeomorphic function of sediment trapping and landform construction. The presence of different functional types and genomes may potentially also lead to the persistence of fluctuating biogeomorphic conditions over larger areas (Stallins, 2005). These relationships between trait diversity and functional stability of BEs require further investigation world-wide.

Criterion 3: testing the hypothesis of niche construction

Landform construction during biogeomorphic succession and related variation in mean trait value and vegetation assemblages are viewed here as an emergent property of ecosystems originating from ecological (10^{-1} to 10^3 years) and evolutionary ($> 10^4$ years) feedbacks between genes, organisms and the geomorphic environment (for more details see Corenblit *et al.*, 2014, 2015). We acknowledge that formal evidence for this statement is lacking, but we stress that the validation of the hypothesis of eco-evolutionary dynamics within BEs has become a priority (e.g. Jones, 2012; Matthews *et al.*, 2014). The proposed models of biogeomorphic succession and biogeomorphic functional similarity at a global scale will help to test the limits of the niche construction hypothesis because they offer a conceptual framework that helps establish a causal relationship between selection of plant traits (response) according to the physical environment and the effects of plant traits on the physical environment.

Management and restoration of BEs

We also stress the opportunity presented by developing this world-wide model of biogeomorphic functional similarity for the restoration and management of BEs. The identification and quantification of key traits leading to establishment of viable

populations of engineer species should become a priority for restoration in relation to their ability to increase ecosystem stability, specifically in the context of global change. The identification and ‘use’ of target response, effect and feedback traits associated with engineer plant species may represent a more efficient solution than the taxonomic approach for ‘manipulating’ the resistance and resilience of BEs in the context of global environmental change. Comprehension and quantification of the natural dynamics of BEs to restore their dynamic biogeomorphic equilibrium according to the reciprocal dependence between engineer plant traits, independently of their biogeographic origin (i.e. native or exotic species) and a changing physical disturbance regime, offers great perspectives for orienting BEs gradually toward suitable target ecological states. The use of the traits of engineer species in such an ecological engineering context may promote sustainable restoration of services to society, such as buffering against erosion and inundation (e.g. Byers *et al.*, 2006; Crain & Bertness, 2006; Temmerman *et al.*, 2013). In the context of global environmental change, the question of which level (i.e. genes, population, community or landscape) should be manipulated will certainly become crucial.

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BIOSKETCH

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