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

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1 **Engineer pioneer plants respond to and affect geomorphic constraints**
2 **similarly along water-terrestrial interfaces worldwide**

3

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20

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33 **ABSTRACT**

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

44 **Location:** Dynamic river and coastal ecosystems worldwide.

45 **Method:** Drawing from a pre-existing model of 'fluvial biogeomorphic succession', we
46 propose a conceptual framework showing that fluvial and coastal 'biogeomorphic
47 ecosystems' are functionally similar due to eco-evolutionary feedbacks between
48 plants and geomorphology.

49 **Results:** The relationships between plant traits and their geomorphic environments
50 within the different fluvial and coastal biogeomorphic ecosystems are identified and
51 classified within a framework of biogeomorphic functional similarity according to three
52 criteria: (i) pioneer plants develop specific responses to the geomorphic environment;
53 (ii) engineer plants modulate the geomorphic environment; (iii) geomorphic changes
54 under biotic control within biogeomorphic ecosystems feed back to organisms.

55 **Main conclusions:** The conceptual framework of functional similarity proposed here
56 will improve our capacity to analyse, compare, manage and restore fluvial and
57 coastal biogeomorphic ecosystems worldwide by using the same protocols based on
58 the three criteria and the four phases of the biogeomorphic succession model.

59

60

61 INTRODUCTION

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

70 The structure and function of any physically disturbed fluvial or coastal ecosystem
71 (e.g. meso to macrotidal conditions along the coast, piedmont to plain river reaches)
72 result from feedbacks between plant dynamics and motion of water, wind, and
73 sediment. Based on the strong feedbacks between plants and geomorphology, Balke
74 *et al.* (2014) recently termed fluvial and coastal ecosystems ‘biogeomorphic
75 ecosystems’ (BE), implying that ecosystem structure and function (i.e. habitat
76 properties and species assemblages; matter and energy fluxes) are emergent
77 properties of plant-geomorphic feedbacks. These feedbacks exist because of the
78 ability of plants to adjust their characteristics to a geomorphologically-dynamic
79 environment by genotypic or phenotypic adaptation, enhancing connectedness (i.e.
80 degree to which the integrity of an ecosystem is controlled through internal feedbacks
81 between small and large scale processes), and resistance and resilience (i.e. ability
82 of the system to recover from physical disturbances) (see Holling, 1973). The BEs we
83 define here relate exclusively to ‘geomorphologically dynamic ecosystems’, which are
84 unstable and subject to frequent and regular physical disturbance. The BE concept is
85 directly related to the ‘fluvial biogeomorphic succession’ (Corenblit *et al.*, 2007,
86 2009a), which encompasses four phases of matter and energy organization in space
87 and time (i.e. geomorphic, pioneer, biogeomorphic, ecological; Fig. 2). Each phase is
88 linked to different time- and space-limited ecosystem structures and functions and is
89 characterized by a specific set of interactions and feedbacks between plants and
90 geomorphology.

91 The *geomorphic phase* is the rejuvenation phase following a flood, storm or tsunami,
92 during which landform properties and stability are mainly defined by hydrodynamic
93 and aerodynamic forces and intrinsic sediment cohesiveness. During this phase, the
94 geomorphic environment controls plant diaspore dispersal (Fig. 2). During the
95 *pioneer phase*, vegetation recruitment occurs on newly formed bare sediment
96 surfaces, and the geomorphic environment controls seed germination and seedling
97 survival and growth (Fig. 2). During the *biogeomorphic phase*, strong feedbacks

98 occur between plant and geomorphic dynamics as morphological and biomechanical
99 characteristics of plants strongly interact with substrate cohesion and geomorphic
100 flows of matter and energy. In the absence of major physical disturbances, changes
101 in the geomorphic environment under the control of and resulting feedback on plants,
102 result in the stabilization of the ecosystem during the *ecological phase* where biotic
103 interactions dominate (Fig. 2).

104 It has been suggested that the ‘fluvial biogeomorphic succession’ model is relevant to
105 dynamic rivers (Davies and Gibling, 2013; Gurnell, 2014; Bätz *et al.*, 2015), and also
106 coastal (Kim, 2012; Balke *et al.*, 2014), and terrestrial BEs (e.g. lateral moraines,
107 Eichel *et al.*, 2013), implying that it could be a useful common foundation for
108 investigating many geomorphically dynamic ecosystems. However, this wide range of
109 applicability does not imply that the quantity and intensity of interactions of plant -
110 geomorphology feedbacks are the same in each BE because: (i) many different taxa
111 and floristic assemblages are observed according to local and regional settings; (ii) at
112 the same location, divergent trajectories in plant community assemblages can occur
113 during the biogeomorphic succession, reflecting variations in initial biological and
114 physical conditions; (iii) the duration and spatial extension of each phase of the
115 biogeomorphic succession varies with the disturbance regime; (iv) different feedback
116 loops exist between plants and geomorphology and related biogeomorphic stability
117 according to the disturbance regime and plant characteristics.

118 Although BEs differ widely taxonomically around the world, comparable constraints
119 can lead to convergent patterns of adaptive *traits* developing across taxa, as implied
120 by the functional framework of adaptive CSR strategies proposed by Grime (2001). A
121 ‘trait’ is any morphological, biomechanical, physiological or phenological feature,
122 measurable at the individual level, from the cell to the whole-organism (Violle *et al.*,
123 2007). Many pioneer plant species have homologous traits optimizing their capacity
124 for reproduction, survival and growth (i.e. fitness) within areas exposed to water, wind
125 and sediment flows (Hesp, 1991; Bornette *et al.*, 2008). This does not mean that all
126 co-occurring species have the same characteristics; alternative strategies may co-
127 occur to cope with a stress, causing a few response trait-groups to co-inhabit a
128 specific habitat (Stallins, 2005; Puijalón *et al.*, 2011).

129 We suggest that fluvial and coastal BEs are functionally similar as a result of
130 dominant feedback mechanisms between the geomorphic environment and plant
131 *response, effect* and *feedback* traits. Here, *response traits* are any plant attributes
132 that provide an adaptive response to water or wind flow, sediment erosion,
133 transportation and deposition, and lead to successful dispersal, recruitment,
134 establishment and reproduction. *Effect traits* are morphological and biomechanical
135 plant traits that induce a significant effect on the geomorphic environment. Within
136 BEs, response and effect traits are strongly linked and may coincide because

137 successful colonization is a prerequisite for plants to affect the geomorphic
138 environment and create biogeomorphic feedbacks. For example, a multi-stemmed
139 flexible morphology may increase the capacity of a plant to resist hydrodynamic
140 forces (response) while also affecting sediment fluxes and topography (effect). We
141 define *feedback traits* as those that provide a response to the modification they
142 induce in the geomorphic dimensions of their niche.

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

149 The trait-based approach we propose here to define a BE is founded on three key
150 criteria related to the geomorphic setting and to the nature of its relation with plants
151 (Fig. 3): (1) plants must have developed specific response traits to the geomorphic
152 environment and its disturbances; (2) they must display effect traits that control the
153 geomorphic environment; (3) they must display feedback traits to these biotic-
154 controlled geomorphic changes. In the presence of a biogeomorphic ecosystem
155 *sensu stricto*, all three criteria have to apply to the plants. In this paper the term 'trait'
156 (response, effect and feedback) will be used as recommended by Violle *et al.* (2007)
157 specifically at the level of individuals. However, responses, effects and feedbacks
158 can relate to varying spatio-temporal levels including individuals (i.e. plastic and
159 evolutionary adjustments of traits), populations (i.e. changes in survival-mortality
160 ratio, age structure, cover) and communities (i.e. adjustments in short and long-term
161 floristic assemblages and biodiversity).

162 **CRITERION 1: RESPONSE TRAITS OF PIONEER PLANTS TO THE** 163 **GEOMORPHIC ENVIRONMENT**

164 **BEs are unstable and subjected to a physical disturbance regime**

165 Most fluvial and coastal BEs consist of unconsolidated sediment and are subjected to
166 a natural disturbance regime (i.e. variations in river water flow, tidal currents and
167 waves, or wind), incorporating both low to medium magnitude variations in
168 hydrodynamic and aerodynamic forces, and also less predictable medium to high
169 magnitude exceptional fluctuations during extreme events (Naiman *et al.*, 2008).
170 Within rivers, the disturbance regime corresponds to seasonal variations in water
171 level and velocity and medium intensity flow pulses, and isolated intense flood
172 events. Within salt marshes and mangroves, it corresponds to daily and seasonal
173 variations in tidal water level and isolated storm or tsunami events. Within coastal

174 dunes, it relates to seasonal variations in extratropical and tropical storm tracks,
175 mean wind velocity and direction, and isolated storm and tsunami events (Balke *et*
176 *al.*, 2014).

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

188 **The disturbance regime acts as an environmental filter of response traits**

189 Engineer plant response traits adapt over the long term to the most regular
190 component of the physical disturbance regime (Lytle & Poff, 2004; Naiman *et al.*,
191 2008). At the establishment stage, selection among the pool of species reflects
192 response traits that favour high net productivity, dispersal, reproduction and survival
193 rates. Many pioneer riparian and coastal species share equivalent response traits
194 (e.g. sexual/vegetative reproduction; body and seed size) related to their morphology,
195 physiology and phenology (Table 1). Plant trait optimization to water, wind and
196 sediment flows does not necessarily result in convergence, but may also cause
197 divergence of traits based on the disturbance regime, resulting in contrasts in the way
198 pioneer plants and flows interact and modulate geomorphic processes and landforms
199 (Bouma *et al.*, 2005, 2013; Stallins, 2005). At the earlier stages of the biogeomorphic
200 succession, and in comparison to biological disturbances such as grazing and
201 bioturbation by animals, the disturbance regime represents the pre-eminent selection
202 pressure for riparian and coastal plants (1 in Fig. 3). It acts as a strong environmental
203 filter of response traits throughout the biogeomorphic succession (Fig. 2; Table 1).

204 Pioneer plants can respond to physical disturbances and sustain viable populations
205 through resistance and resilience mechanisms (Table 1), where resistance is the
206 capacity of the plant to maintain its structure or biomass during disturbances, and
207 resilience is the capacity of the plant to restore its structure or biomass after
208 disturbances. In many cases high frequency disturbances of low to medium intensity
209 are essential for the expression of response traits favouring plant resistance and
210 resilience within fluvial and coastal BEs.

211 **Plant response traits during the geomorphic phase**

212 During the geomorphic phase, the geomorphic environment controls the biotic
213 compartment (Fig. 2), especially diaspore dispersal, which is a crucial process that
214 may coincide with predictable (seasonal) hydrogeomorphic or aerodynamic
215 conditions that guarantee successful recruitment. Recruitment of pioneer populations
216 in BEs requires the coincidence of diaspore release with adequate abiotic conditions.
217 Phenological response traits of many plant species are intimately coupled to the
218 periodicity and intensity of hydrogeomorphic constraints (Bornette *et al.*, 2008; Maun,
219 2009; Balke, 2013; Table 1). In order to cope with the inherently stochastic nature of
220 the geomorphic phase, pioneer engineer plants generally employ opportunistic
221 strategies (*sensu* Grime, 2001; Table 1). Diaspores are mostly produced in very large
222 numbers and can remain viable for a long period. Their production and release are
223 usually well synchronized with the disturbance regime and climate patterns. For
224 example, within temperate river environments seed production and release by
225 riparian *Populus* and *Salix* spp. coincides with the period following predictable annual
226 floods (Lytle & Poff, 2004; Stella *et al.*, 2006) so that their small, buoyant seeds are
227 transported by water and wind to newly-formed bare sediment surfaces. In coastal
228 environments, diaspores (seeds, rhizomes, stolons, roots and branches) are mainly
229 hydrochorous (Table 1). They are mobilized and transported by water, usually during
230 floods and storms (Maun, 2009), and they maintain their capacity to germinate and
231 sprout after transportation in salty water (Guja *et al.*, 2010). Within mangroves formed
232 by *Rhizophora* and *Avicennia* spp., massive propagule production occurs during the
233 wet season when salinity is low (Fernandes, 1999). Within coastal dune BEs, certain
234 annual species release large quantities of seeds during the period with the highest
235 availability of bare moist coastal substrates that are required for seed germination
236 (Wagner, 1964).

237 **Plant response traits during the pioneer phase**

238 The transition toward more vegetated states that accompanies amelioration of the
239 harsh abiotic environment is highly variable because initial habitat conditions strongly
240 affect initial plant establishment, and the transition requires adequate physical
241 conditions related to combinations of morphological, biomechanical and physiological
242 response traits (Table 1), and also proximity to a diaspore source or dispersal
243 pathway. In rivers (Cooper *et al.*, 2003), salt marshes and mangroves (Balke *et al.*,
244 2014), dynamic interactions between numerous fluctuating climatic and
245 geomorphologic parameters lead to multiple possible pathways of seedling
246 recruitment on bare surfaces that are only colonised in sufficient numbers every few
247 years. Recruitment success can change with quite small variations in
248 hydrogeomorphic parameters. Similarly, in dune settings, seedling recruitment
249 depends upon the contrasts in wave energy under winter and summer wave regimes

250 and the net balance between seasonal patterns of sediment erosion and deposition
251 with subsidies from seaweed and other organic wrack debris enhancing the likelihood
252 of seedling recruitment (Davidson-Arnott & Law, 1990).

253 Once seeds and propagules (e.g. rhizomes, stolons, roots) of pioneer engineer
254 species reach a freshly exposed, bare surface they germinate or anchor almost
255 immediately, whether on alluvial bars within fluvial BEs (Gom & Rood, 1999), on mud
256 flats within mangroves (Guja *et al.*, 2010) or on the upper beach within coastal dune
257 BEs (Maun, 2009). Many riparian (e.g. *Populus* and *Salix* spp.), salt marsh (e.g.
258 *Spartina* and *Puccinellia* spp.) and mangrove tree (*Sonneratia* and *Avicennia* spp.)
259 species are highly clonal. The ability to easily resprout is a major advantage for
260 colonizing areas heavily disturbed by extreme disturbance events.

261 During the early stage of the biogeomorphic succession, emerging seedlings or
262 sprouts remain highly exposed to fluctuating hydrodynamic and aerodynamic forces,
263 sediment dynamics and substrate moisture (Mahoney & Rood, 1998; Bouma *et al.*,
264 2009; Balke *et al.*, 2014). Following germination, rooting anchorage may develop
265 very quickly ensuring a strong, early mechanical and physiological resistance to
266 hydrodynamic or aerodynamic forces, sediment burial or to stress induced by ground
267 and soil water fluctuation (Westelaken & Maun, 1985; Guilloy *et al.*, 2011). For
268 example, many vivipar propagules of mangrove trees have pre-formed roots that
269 ensure almost immediate anchoring and morphological plasticity is already important.
270 Balke *et al.* (2013) showed that sediment burial increases shoot growth and erosion
271 increases root growth of mangrove tree seedlings, increasing their survival chances
272 according to the disturbance regime. Seedling growth rate is also crucial. Balke *et al.*
273 (2014) identified two conditions for successful recruitment within fluvial and coastal
274 BEs: (i) the coincidence of dispersal events with sufficient hydrodynamic or
275 aerodynamic force to bring an adequate number of diaspores to suitable sites; (ii) a
276 sufficiently long period for seedlings to germinate and establish that is free of
277 destructive disturbances. This window of opportunity can be a few days to a few
278 months in fluvial BEs and a few hours to a few days within salt marshes, mangroves
279 and coastal dunes (Balke *et al.*, 2014). Therefore, colonization events can potentially
280 be predicted when plant response trait information on germination, root growth and
281 plant stability are linked to environmental variables such as water level, wind speed
282 and salinity.

283 **Plant response traits during the biogeomorphic phase**

284 Plants that are adapted to unstable and fluctuating geomorphic environments have
285 high phenotypic variability and plasticity, including modulation of above and
286 belowground biomass allocation, architecture, and the biomechanical and
287 physiological properties of organs, which ensure their resistance to water flow and

288 wind, sediment erosion, burial and sand abrasion (Bornette *et al.*, 2008; Maun, 2009;
289 Table 1). Trait changes result from trade-offs between the need to resist abrasive and
290 tractive mechanical forces, prolonged submersion, and sediment erosion and burial;
291 to acquire resources; and to adapt their reproductive strategy (clonal vs. sexual) to
292 disperse and establish efficiently.

293 Response traits that support resistance to mechanical constraints are mainly
294 morphological and biomechanical, including strengthening tissues; stiff stems; prop,
295 stilt and kneed roots; small and streamlined leaves and canopies; brittle stems with
296 breaking points (Bouma *et al.*, 2005; Bornette *et al.*, 2008; Maun, 2009; Table 1).
297 Pioneer plants are highly resilient to damage. For example, they can resprout from
298 damaged stumps and rhizomes (Nzunda *et al.*, 2007; Moggridge & Gurnell, 2009), or
299 they can show a plastic morphological and biomechanical response (i.e.
300 thigmomorphogenesis) to repetitive mechanical forces from water or wind, increasing
301 their resistance to breakage and uprooting. Response trait variations can express a
302 trade-off between tolerance (e.g. large stem cross-section, production of
303 strengthening tissues, increase in root biomass) and avoidance (e.g. increase in stem
304 flexibility, aerial biomass reduction, morphological reconfiguration within the fluid)
305 (Puijalon *et al.*, 2011), and can have major consequences for a plant's ability to fit to
306 disturbance (Bouma *et al.*, 2005; Stallins, 2005; Gurnell, 2014). In the case of
307 absence of major disturbances, the biogeomorphic phase can be followed by the
308 ecological phase where biotic interactions (e.g. competition) are dominant and
309 physical disturbances rare.

310 **CRITERION 2: EFFECT TRAITS OF ENGINEER PLANTS THAT MODULATE THE** 311 **GEOMORPHIC ENVIRONMENT**

312 Within BEs, the control of ecosystem structure and function by engineer plants is
313 achieved through durable modification of the habitat (2 in Fig. 3). Three main
314 categories of effects of engineer plants on their geomorphic environment can be
315 identified and are explored further below: (i) increase in sediment retention and
316 cohesiveness; (ii) fluid stress divergence; and (iii) physicochemical modification and
317 biogenic accumulation.

318 **Increase in sediment retention and cohesion**

319 In fluvial and coastal BEs, the roots and rhizomes of plants increase sediment
320 cohesiveness (Polvi *et al.*, 2014), offering protection against erosion, particularly
321 where pioneer plants have dense root systems and flexible, flattening or creeping
322 canopies. A very-well developed literature demonstrates how such engineer plants
323 obstruct water and wind flows, reducing shear stresses at the ground surface and
324 trapping matter 'within-site' (within their canopy) and 'off-site' (downstream or

325 downwind of the vegetation stand). Within-site effects on sediment trapping and the
326 extent of downstream or downwind deposition vary with canopy structure, fluid
327 properties, and sediment transport (Bouma *et al.*, 2013; Nardin & Edmonds, 2014).
328 Individual woody plants or isolated herbaceous patches locally impact sediment
329 transport forming small hummocks or coppice dunes. Isolated groups of dense
330 ligneous and herbaceous perennials form pioneer islands and discontinuous benches
331 at river channel margins (Gurnell *et al.*, 2012); large hummocks within salt marshes
332 (Bouma *et al.*, 2009); islands and platforms within mangroves (Fromard *et al.*, 2003);
333 and large coppice dunes, incipient foredunes or parabolic dunes within coastal dune
334 systems (Baas, 2007; Hesp & Martínez, 2008). At larger spatial and temporal scales,
335 between catastrophic floods, storms and tsunamis, engineer plants interact with
336 sediment transport to create large stabilized vegetated islands and floodplains in
337 fluvial BEs, and plain dunes and inter-tidal stabilized flats in coastal BEs. Pioneer
338 biogeomorphic units also induce off-site effects by protecting downstream and
339 downwind areas and allowing further recruitment. This is illustrated, for example, by
340 the way in which pioneer islands colonized by *Populus nigra* and *Salix* spp. within the
341 high-energy Tagliamento river (Northern Italy) enhance seedling and sapling survival
342 in sheltered areas (Moggridge & Gurnell, 2009).

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

362 **Fluid stress divergence**

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

375 The combination of local and downstream or downwind protective-accretive and off-
376 site erosive effects of plants control spatial and temporal self-organization of BEs
377 mainly during the biogeomorphic phase (Temmerman *et al.*, 2007; Bouma *et al.*,
378 2009, 2013; Kim, 2012; Corenblit *et al.*, 2015). It has been further suggested that the
379 pattern of sediment trapping and erosion corresponds to a biogeomorphic scale-
380 dependent feedback. Such feedbacks occur within ecosystems when the landform
381 pattern is reinforced and maintained by a positive feedback in resource acquisition at
382 the local scale (within-site) and when an inhibiting feedback occurs at a larger scale
383 (off-site, at the margins). Evidence for the landscape consequences of scale-
384 dependent feedbacks in BEs is especially strong for rivers (Gurnell, 2014) and salt
385 marshes (Temmerman *et al.*, 2007; Bouma *et al.*, 2009, 2013), although
386 biogeomorphic self-organization also occurs within sand-dune systems (Baas, 2007).

387 **Physicochemical modification and biogenic accumulation**

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

392 For example, in high energy rivers, Bätz *et al.* (2015) showed how organic matter
393 input within stabilized pioneer landforms enhance the transition from landforms
394 dominated by fresh sediment deposits towards soil-covered biogeomorphic units
395 such as floodplains. Within salt marshes and mangroves, where the tidal range and
396 the minerogenic sediment input are limited, engineer plants alter the topography
397 through peat-like substrate formation. Morris *et al.* (2002) suggested that coastal
398 engineer plants can control their relative elevation through biomass modulation in

399 order to keep up with sea-level rise. Several studies have also shown that many salt
400 marshes and mangroves are able to maintain their surface elevation within the inter-
401 tidal zone over long periods of sea level rise through the modulation of root and aerial
402 biomass production by plants, and associated peat formation and vertical land-
403 building (Larsen & Harvey, 2010; Marani *et al.*, 2013). Furthermore, fixed dune
404 systems are characterized by the existence of soil catenas that reflect feedbacks
405 between sediment characteristics, topography, drainage conditions and vegetation
406 (Maun, 2009).

407 **CRITERION 3: FEEDBACK TRAITS ASSOCIATED WITH BIOTIC-CONTROLLED** 408 **GEOMORPHIC CHANGES**

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

415 **Individual and population plant response to sediment accretion they enhance**

416 Many pioneer engineer plant species that establish within fluvial and coastal BEs
417 require sediment burial to enhance their anchorage, to favour more vigorous growth,
418 and to increase their chances of reaching sexual maturity (Maun, 2009; Corenblit *et al.*,
419 2014). One or more plant individuals that initiate formation of an embryo fluvial or
420 coastal island, a small shadow dune, or a tussock, can exploit the freshly deposited
421 sediment by developing adventitious roots and rhizomes to stabilize a viable
422 population in a geomorphologically-unstable environment (Maun, 2009; Rood *et al.*,
423 2011), and lead at the micro- to meso-scales to a positive feedback of landform
424 construction, vegetation growth (i.e. feedback traits) and population demographic
425 stabilization. This is exemplified by *Populus* and *Salix* spp. within river environments
426 (Corenblit *et al.*, 2014; Gurnell, 2014), subspecies of *Spartina patens* within salt
427 marshes (Wolner *et al.*, 2013) and *Avicennia germinans* in mangroves (Fromard *et al.*,
428 2003). This is also well exemplified in coastal dunes by grass species. For
429 example, Zarnetske *et al.* (2012) noted that aerial growth of pioneer engineer plants
430 is favored by sediment deposition they enhance in coastal dunes of the Pacific
431 Northwest of the USA. Vertical canopy growth was observed to be stimulated within a
432 few weeks following burial, and the dune building capacity of engineer species was
433 linked to a specific biogeomorphic feedback between plant growth and architecture,
434 and sediment deposition.

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

447 **Plant community response to geomorphic changes**

448 Sediment accretion and related topographic aggradation under the control of
449 engineer plants also control plant assemblages at community level through the
450 exclusion of species by burial, the decrease of exposure to disturbance and
451 vegetation shading (Corenblit *et al.*, 2014, 2015). Within rivers and coastal BEs, it is
452 the combination of sediment accretion, topographic rise and vegetation growth that
453 leads to the main changes in the physicochemical properties of the habitat and in
454 floristic assemblages during the biogeomorphic phase (Tabacchi *et al.*, 2000; Gurnell,
455 2014). For example, when foredunes develop within coastal dunes, they lower the
456 amount of sand and salt spray transported inland, facilitating the incursion of woody
457 vegetation in their lee-protection. At the same time, as control by physical constraints
458 diminishes, biogeochemical controls become prominent, with organic matter
459 accumulation and shifts in habitat diversity from a horizontal (within the habitat
460 mosaic) to a vertical (soil to canopy) development (Bätz *et al.*, 2015).

461 **Eco-evolutionary feedbacks**

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

469 Therefore, the geomorphic gradients and associated community assembly rules and
470 functional structure that are observed within fluvial and coastal BEs, need to be
471 considered as emergent properties of short-term (ecological) and long-term (eco-

472 evolutionary) top-down and bottom-up abiotic-biotic feedbacks (Corenblit *et al.*,
473 2015). Recent palaeontological studies (e.g. Davies & Gibling, 2013) have shown
474 that the evolutionary trajectory of engineer plant traits and many other passenger
475 taxa (microorganisms, fauna and flora) has been modulated over the long term within
476 fluvial BEs by the niche-constructing activity of engineer plants and the resulting
477 network of diffuse co-evolution among the different taxa (Corenblit *et al.*, 2014, 2015).
478 Consequently, eco-evolutionary (*sensu* Erwin, 2008) concepts such as niche
479 construction (Odling-Smee *et al.*, 2003) certainly represent a useful framework for
480 analyzing feedbacks between organisms and geomorphology within fluvial and
481 coastal BEs.

482 **FUTURE RESEARCH TASKS**

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

490 **Criterion 1: defining the window of opportunity of engineer species**

491 The habitat conditions leading to successful germination and growth of key engineer
492 species must be quantified *in situ*. The quantification of the factors affecting
493 recruitment of plants within fluvial and coastal environments has begun a long time
494 ago. The 'recruitment box' model for fluvial systems of Mahoney & Rood (1998) and
495 the homologous model of a 'window of opportunity' for all four biogeomorphic
496 ecosystems proposed by Balke *et al.* (2014) emerged from previous studies. They
497 are both useful operational conceptual frameworks for analyzing the relationship
498 between environmental variability and vegetation recruitment during the pioneer
499 phase of the biogeomorphic succession. The hierarchy of the same local and
500 regional factors affecting plant dispersal, germination, initial growth and survival in
501 different world locations must be established. Response traits that provide an
502 advantage must be identified and quantified simultaneously *in situ* and *ex situ* in
503 controlled conditions to isolate the key factors (e.g. Guilloy *et al.*, 2011; Balke *et al.*,
504 2014). Quantitative comparison between different BEs will lead to a formal definition
505 of the worldwide envelope of environmental conditions leading to successful
506 recruitment of engineer plant species that can modulate their geomorphic
507 environment. The frequency histogram of the number (and related functional status)
508 of recruited engineer species along geomorphic niche dimensions, such as for

509 example mean duration and frequency of disturbances, will be a useful tool for
510 identifying functional groups of response to geomorphic constraints.

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

517 **Criterion 2: linking plant traits and landform properties**

518 Establishing quantitative understanding of the relation between engineer plant
519 response, effect and feedback traits, and landform geometry, dynamics and
520 physicochemical properties is also a priority. Effects of engineer plants on
521 geomorphology must be quantified by considering causal linkages with resulting
522 feedback traits. We consider that the geometrical and physicochemical properties of
523 each category of small to large scale coastal and fluvial landforms (e.g. pioneer
524 fluvial or mangrove islands, hummocks, copies dunes and foredunes) are modulated
525 across the world by the same basic processes but according to specific traits of the
526 local pioneer engineer plant species. These landforms that develop under the control
527 of engineer plants thus exhibit a large range of possible deviations in size, shape,
528 texture, physicochemical characteristics, resistance and resilience relative to their
529 theoretical physical state. Such deviations are likely to be biologically functional for
530 the engineer species and potentially for passenger species. Therefore, it is an
531 important goal to test the hypothesis of engineered landform functionality at the
532 global scale (Corenblit *et al.*, 2015). This will be achieved by analyzing correlations
533 between plant growth performance and type of reproduction, and the frequency
534 histogram of landform properties such as relative elevation, exposure to disturbances
535 (Bertoldi *et al.*, 2011) and physicochemical properties (Bätz *et al.*, 2015). Ultimately,
536 the correspondence between genetic variability of engineer plant species and
537 landform properties must be analyzed to establish a genetic basis of the variation of
538 landform geometry and dynamics.

539 Another important research objective related to criterion 2 is to test the effects of
540 plant trait diversity on the function of landform construction and ecosystem
541 stabilization. Plant functional traits enhancing sediment cohesiveness and trapping
542 often combine at the community level and form functional units with varying sediment
543 stabilization and trapping capacities (Corenblit *et al.*, 2009b). Population thresholds
544 of sediment stabilization and trapping might be overridden by the combination of
545 different traits at the community scale. The combination of varying traits, and thus
546 varying genomes, is likely to increase the stability of the biogeomorphic function of

547 sediment trapping and landform construction. The presence of different functional
548 types and genomes may potentially also lead to the persistence of fluctuating
549 biogeomorphic conditions over larger areas (Stallins, 2005). These relationships
550 between trait diversity and functional stability of BEs require further investigation
551 worldwide.

552 **Criterion 3: testing the hypothesis of niche construction**

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

566 **Biogeomorphic ecosystem management and restoration**

567 We also stress the opportunity presented by developing this worldwide model of
568 biogeomorphic functional similarity for the restoration and management of BEs. The
569 identification and quantification of key traits leading to establishment of viable
570 populations of engineer species should become a priority for restoration in relation to
571 their increase of ecosystem stability, specifically in the context of global change. The
572 identification and 'use' of target response, effect and feedback traits associated with
573 engineer plant species may represent a more efficient solution than the taxonomic
574 approach for 'manipulating' BE resistance and resilience in the context of global
575 environmental change. Comprehension and quantification of the natural dynamics of
576 BEs to restore their dynamic biogeomorphic equilibrium according to the reciprocal
577 dependency between engineer plant traits, independently from their biogeographic
578 origin (i.e. native or exotic species) and a changing physical disturbance regime,
579 offers great perspectives for orienting BEs gradually toward suitable target ecological
580 states. The use of engineer species traits in such an ecological engineering context
581 may promote sustainable restoration of services to society such as buffering against
582 erosion and inundation (e.g. Byers *et al.*, 2006; Crain & Bertness, 2006; Temmerman
583 *et al.*, 2013). In the context of global environmental change, the question of which

584 level (i.e. genes, population, community, landscape) should be manipulated will
585 certainly become crucial.

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796

797 **Biosketch**

798

799 The biogeomorphic research group which has collaborated for this article is
800 interested in studying feedbacks between plant dynamics and geomorphology within
801 various fluvial and coastal ecosystems around the world. All authors contributed
802 substantially in writing the article according to their experience of rivers (D. Corenblit,
803 E. González, V. Garófano-Gómez, A.M. Gurnell, B. Hortobágyi, F. Julien, L. Lambs,
804 J. Steiger, E. Tabacchi), salt marshes and mangroves (T. Balke, T. Bouma, D. Kim,
805 F. Fromard, R. Walcker) and coastal dunes (A. Baas, J.A. Stallins).

806

807 **Tables**

808 **Table 1.** Developmental sequence of biogeomorphic ecosystems (BEs) during the biogeomorphic succession and related plant
 809 functional traits. The functional structure of a BE is shaped by a set of plant species specifically adapted to geomorphic
 810 disturbances and to stress. Such species are related, for example within temperate fluvial BEs, to the genera *Alnus*, *Populus*, *Salix*,
 811 and *Tamarix*; within tropical mangrove BEs to *Avicennia*, *Ceriops*, *Rizophora* and *Sonneratia*; within temperate salt marsh BEs to
 812 *Juncus*, *Puccinellia*, and *Spartina*; and within temperate dune BEs to *Ammophila*, *Cakile*, *Panicum*, and *Uniolo*. Many species of
 813 these genera developed similar functional response traits specifically related to regular and ordinary variations in hydrodynamic and
 814 aerodynamic forces and also to a certain range of energy pulses and their subsequent consequences on sediment erosion,
 815 transportation and deposition. Here, the common and specific functional traits of the four different BEs are listed and related to each
 816 biogeomorphic succession 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. convex bar formation during progressive meander migration in rivers) and tides within dynamic coastal zones Punctual at a 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 lifespan; production of numerous buoyant seeds and propagules; seed release synchronized with the flow regime Salt marsh and mangrove: vivipary and floating diaspores (longer lifespan in salty water)

Pioneer	Few days to few months	Establishment of bare surfaces. Geomorphic processes exert a strong and unidirectional control on organisms, filtering community composition	<p>Fluvial BEs: alluvial bar formation</p> <p>Salt marsh and mangrove BEs: tidal mudflat formation</p> <p>Coastal dune BEs: beach accretion</p>	<p>Recruitment</p> <p>Germination and sprouting on open bare sediments; seedling/resprout</p>	Common: rapid root anchoring; clonal growth from drifting debris and propagules; seedling tolerance to submersion and sediment burial
Biogeomorphic	Few years to few decades	Population establishment; engineer plants control geomorphology and respond to changes in geomorphic environment; overall strong feedbacks between biota and the physical environment	<p>Common: sediment accretion within and downstream/downwind vegetation patches</p> <p>Fluvial BEs: pioneer vegetated islands and benches</p> <p>Salt marsh BEs: tussocks, hummocks, vegetated tidal mudflat</p> <p>Mangrove BEs: vegetated tidal mudflat</p> <p>Coastal dune BEs: coppice dunes, hummocks, foredune, parabolic dune</p>	Dominance of engineer plants; facilitation for some other taxa; taxa exclusion; resource grab uptake in a more and more stabilizing habitat	<p>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</p> <p>Fluvial BEs: allocation to belowground biomass and branch sacrifice during the dry season; adaptation to hydrodynamics forces: high bending stability, flexible stems, narrow leaf shape, multi-stemmed resprouting from roots and shoots; brittle twig bases</p> <p>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.</p> <p>Mangrove BEs: adaptations to long submersion in salty water: aerenchyma tissue for transferring oxygen from the atmosphere to submerged roots; pneumatophores; salt excretion and</p>

					<p>exclusion; salt sequestration into leaves periodically shed; adaptation to hydrodynamics forces: spreading horizontal roots, prop and stilt roots, kneed roots</p> <p>Coastal dune BEs: anatomical adaptation to sediment abrasion</p>
Ecological	Few decades to few centuries	Older ecological succession (post-pioneer to mature stabilized stands); BE dominantly structured by biotic interactions	<p>Fluvial BEs: vegetated floodplains and mature islands</p> <p>Salt marsh BEs: raised vegetated tidal mudflat</p> <p>Mangrove BEs: raised vegetated tidal mudflat</p> <p>Coastal dune BEs: stabilized parabolic and plain vegetated dunes</p>	<p>Plant succession</p> <p>Increase of biotic interaction (e.g. competition and positive interactions) such as for example symbiosis)</p> <p>Pedogenesis</p>	<p>Common: development of competitive traits (e.g. high size) to access resources more efficiently and reproduce in a stabilized environment</p>

818 **Figure legends**

819 **Figure 1.** Global distribution of distinct fluvial and coastal biogeomorphic ecosystems
820 (BEs). (a): River abundance by ecoregion defined from low (light blue) to high (dark
821 blue) (Abell *et al.*, 2008), photo: J. Steiger; (b): salt marshes distribution (UNEP
822 WCMC, 2013), photo: T. Balke; (c): mangroves distribution (Giri *et al.*, 2011), photo:
823 T. Balke; (d): coastal dunes distribution (Martínez *et al.*, 2004), photo: J.A. Stallins.

824 **Figure 2.** Conceptual model of biogeomorphic succession (*sensu* Corenblit *et al.*,
825 2007, 2009a). Interactions between the physical (squares) and biological (circles)
826 compartments are shown for each phase (inspired from Odling-Smee *et al.*, 2003).
827 Arrows indicate an interaction with its intensity schematized by the size of line. The
828 influence of engineering plants on the physical compartment is represented by a dark
829 color within the squares. Physical changes related to early stages of the
830 biogeomorphic phase correspond to sediment accretion and topographical raise;
831 those associated with late stages of the biogeomorphic phase and to the ecological
832 phase to changes in physicochemical properties of the soil.

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

840 **Figure 4.** Exposure gradients to hydrogeomorphic and aerodynamic disturbances in
841 fluvial and coastal biogeomorphic ecosystems (BEs). Hydrogeomorphic disturbance
842 is represented in terms of water level variations for all the ecosystems and has
843 different impacts depending on the specific biogeomorphic succession phase
844 (represented in the line at the bottom of each ecosystem). The correspondence with
845 the model of biogeomorphic succession (Fig. 2) is shown at the bottom of the figure.
846

847 **Figures**

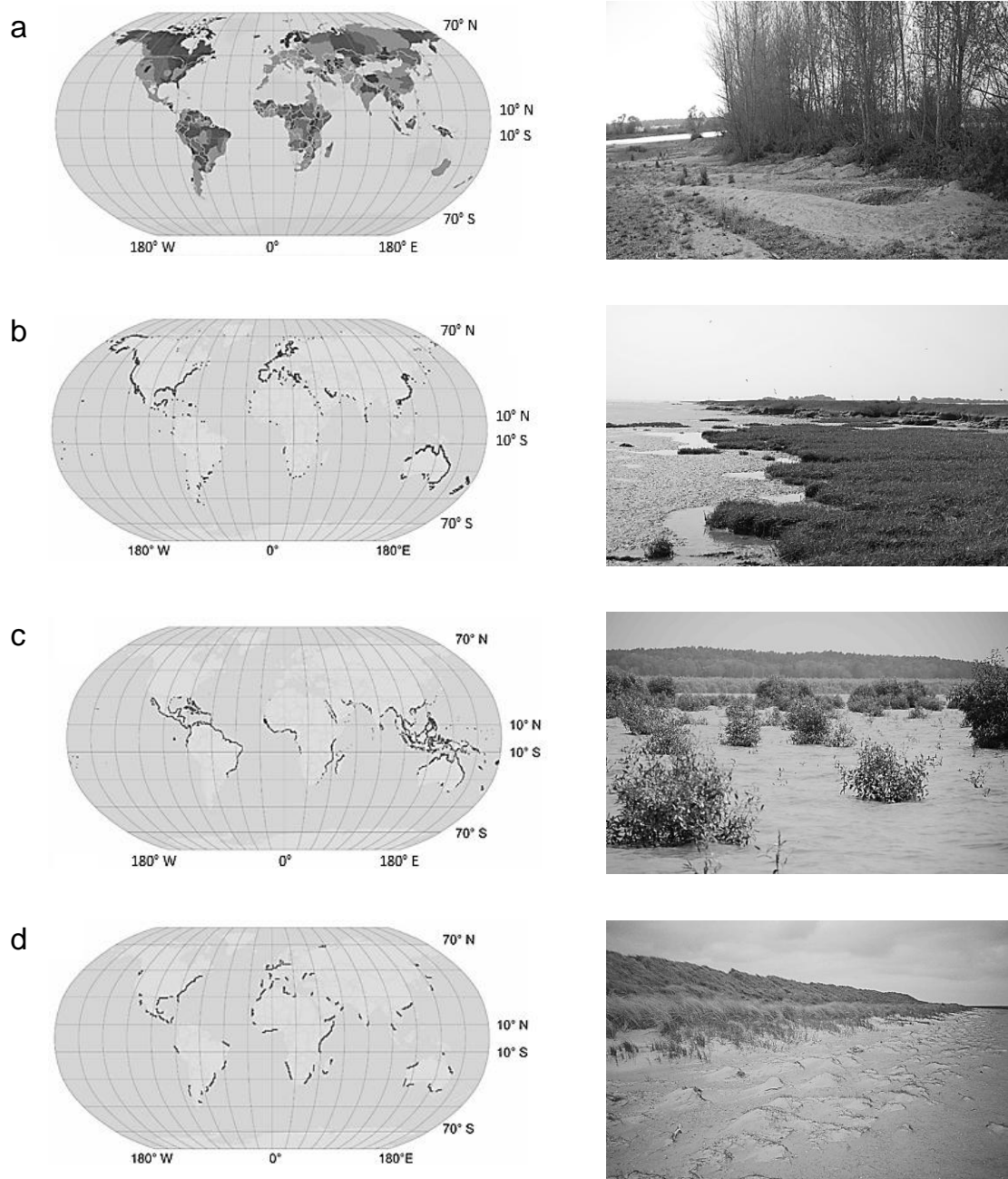
848 Figure 1.

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850 Color fig.

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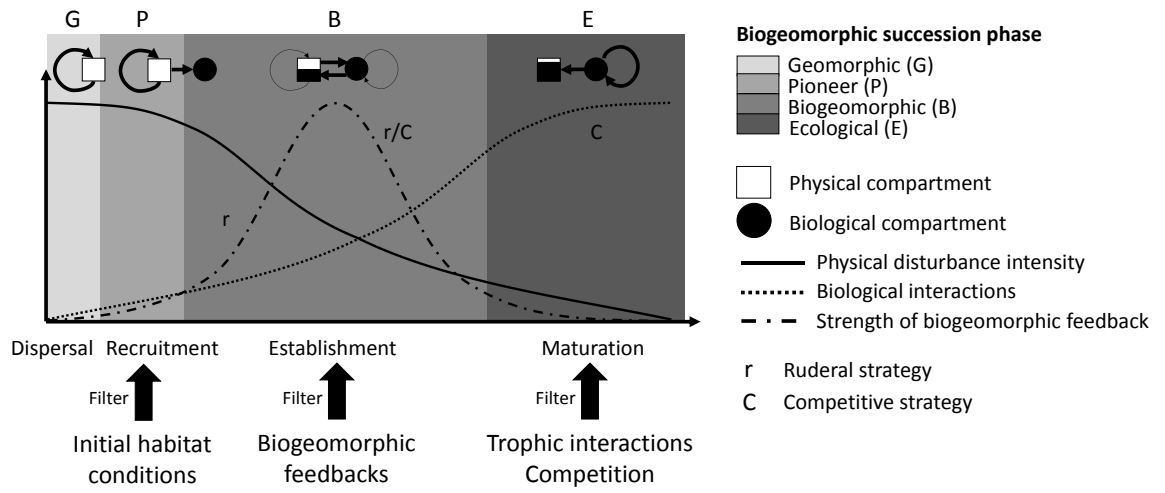
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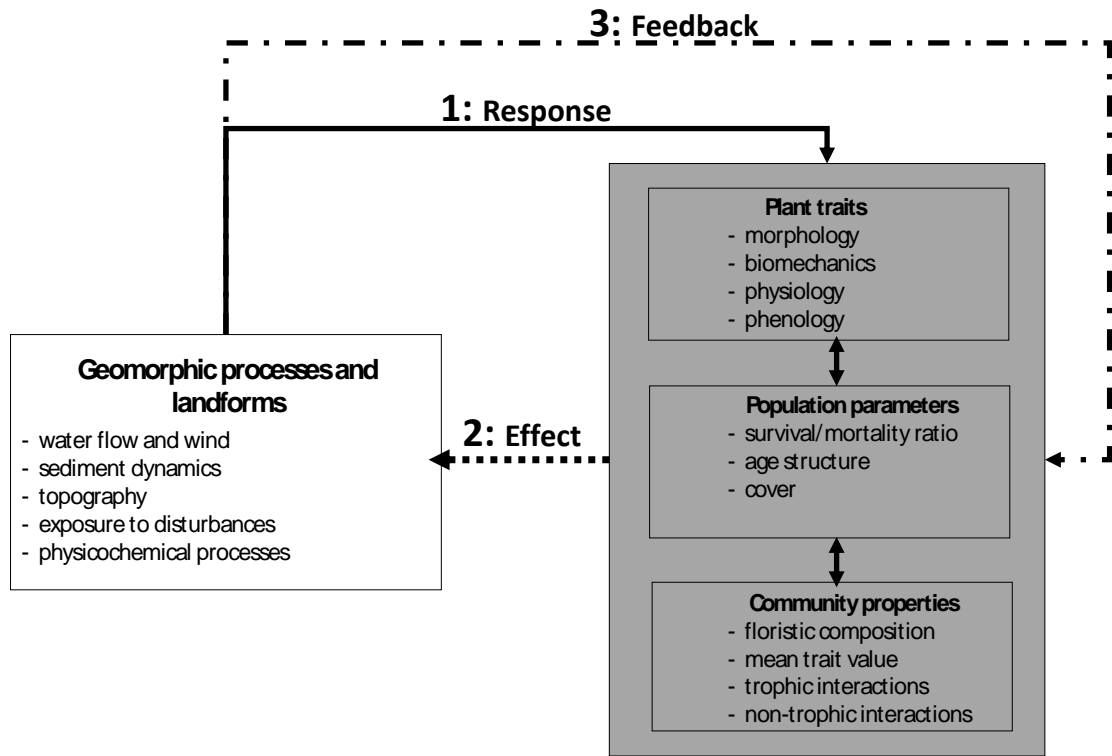
Figure 2.



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Figure 3.

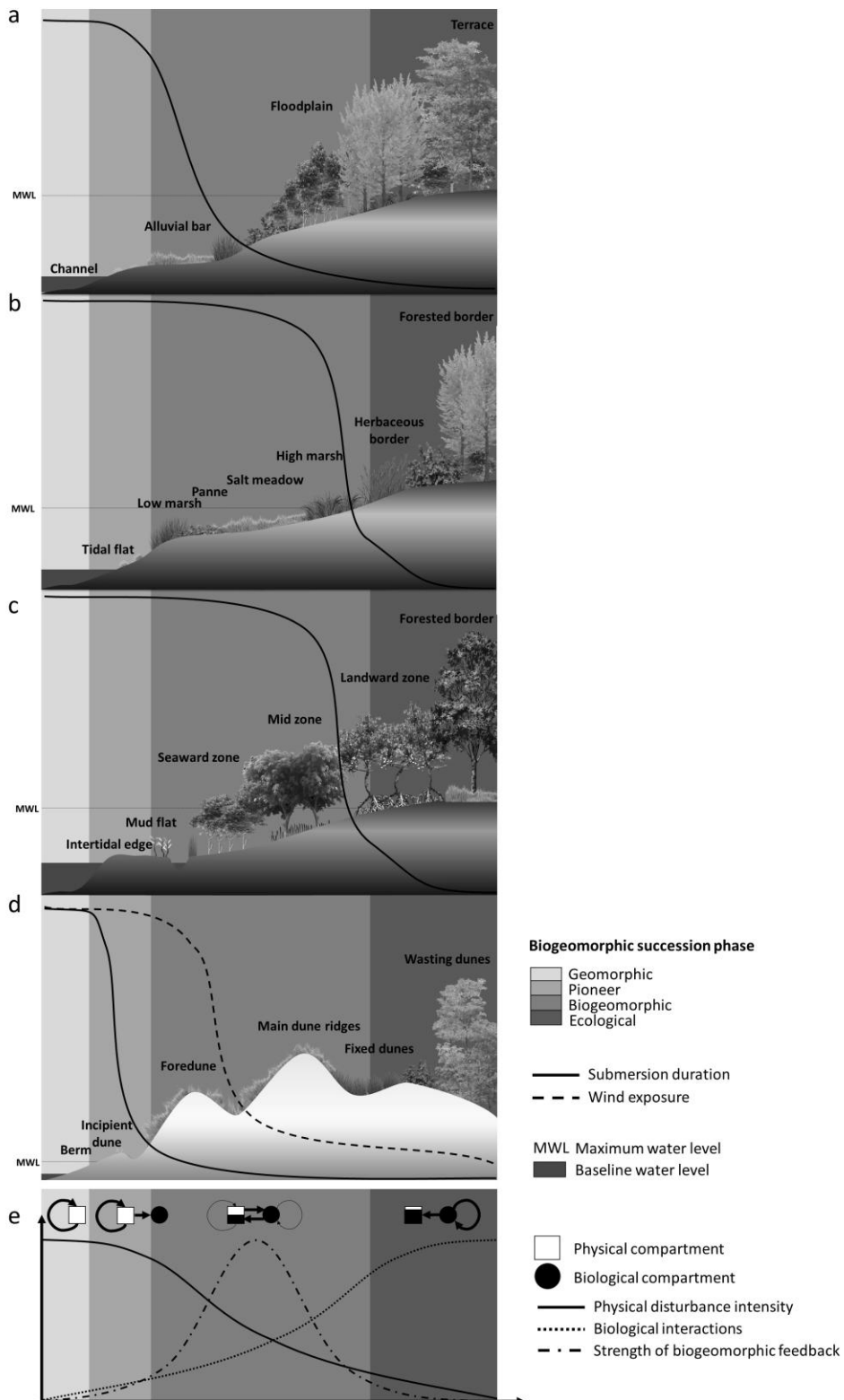


860 Figure 4.

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863 Figure 4.



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