

State of Science

Considering river structure and stability in the light of evolution: feedbacks between riparian vegetation and hydrogeomorphology

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ABSTRACT: River ecological functioning can be conceptualized according to a four-dimensional framework, based on the responses of aquatic and riparian communities to hydrogeomorphic constraints along the longitudinal, transverse, vertical and temporal dimensions of rivers. Contemporary riparian vegetation responds to river dynamics at ecological timescales, but riparian vegetation, in one form or another, has existed on Earth since at least the Middle Ordovician (c. 450 Ma) and has been a significant controlling factor on river geomorphology since the Late Silurian (c. 420 Ma). On such evolutionary timescales, plant adaptations to the fluvial environment and the subsequent effects of these adaptations on fluvial sediment and landform dynamics resulted in the emergence, from the Silurian to the Carboniferous, of a variety of contrasted fluvial biogeomorphic types where water flow, morphodynamics and vegetation interacted to different degrees. Here we identify several of these types and describe the consequences for biogeomorphic structure and stability (i.e. resistance and resilience), along the four river dimensions, of feedbacks between riparian plants and hydrogeomorphic processes on contrasting ecological and evolutionary timescales. Copyright © 2014 John Wiley & Sons, Ltd.

KEYWORDS: fluvial biogeomorphic succession; riparian vegetation; functional effect and response traits; vegetation evolution; scale-dependant feedback; ecosystem engineer; ecosystem resistance and resilience; niche construction

Introduction

Riparian ecosystems, developing at the interface between water and land, are among the most geomorphologically dynamic and variable environments on the Earth surface in terms of structure, function and diversity (Naiman and Décamps, 1997) and strength of abiotic–biotic feedbacks (Corenblit *et al.*, 2007). The biogeomorphic structure and stability of riparian ecosystems are the products of a long and complex history, in which a hierarchy of abiotic–biotic feedbacks developed over hundreds of millions of years.

From a hydrogeomorphic perspective, geomorphologists have long proposed frameworks describing fluvial geomorphic adjustments from the scale of the hydrological basin (Schumm, 1977) to the scale of the river channel (Leopold and Maddock, 1953; Wolman, 1955) (see also Church, 2002; Wohl, 2014). Based on these geomorphic frameworks, hydroecologists have conceptualized river ecological functioning in four dimensions:

longitudinal, transverse, vertical and temporal. This four-dimensional framework was set out by Amoros *et al.* (1987a) (concept of 'fluvial hydrosystems') and Ward (1989).

The four-dimensional framework provides a strong conceptual basis for studying river ecosystem-level functioning on the basis of matter and energy fluxes. Specific conceptual models related to this framework include the river continuum (Vannote *et al.*, 1980), nutrient spiraling (Newbold *et al.*, 1982), flood pulse (Junk *et al.*, 1989), patch dynamics (Townsend, 1989), boundary–interface (Naiman and Décamps, 1997), natural flow regime (Poff *et al.*, 1997), flow pulse (Tockner *et al.*, 2000), and river discontinuum (Poole, 2002). These models postulated that aquatic and riparian community structure could be explained by considering the linkage between the life-history traits of species and the spatiotemporal patterns of hydrogeomorphic processes along the different dimensions (Townsend and Hildrew, 1994). Many studies undertaken within this framework have outlined the huge diversity of aquatic and riparian

communities linked to spatial heterogeneity in hydrogeomorphic parameters and to temporal variability along the river dimensions (Pickett and White, 1985; Poff *et al.*, 1997; Ward *et al.*, 1999; Latterell *et al.*, 2006; Thorp *et al.*, 2006; Bornette *et al.*, 2008).

However, these models were based on a physical habitat template (*sensu* Southwood, 1977) that focused strictly on how hydrogeomorphic heterogeneity and variability affected the biotic compartments. They did not consider explicitly how and to what extent river spatial dimensions adjust at nested spatiotemporal scales under the control of engineer (*sensu* Jones *et al.*, 1994) plant species, which exert profound effects on hydrogeomorphic processes, river geomorphology and habitat conditions. Thus, as suggested by Fisher *et al.* (2007) and Wainwright *et al.* (2011), they overlook, at least to a certain extent, certain aspects of the highly significant role of abiotic–biotic feedbacks linked to aquatic and riparian plant species within river ecological functioning.

Within river corridors, riparian vegetation controls or modulates the patterns of ground and surface water (Tabacchi *et al.*, 2000), fine sediment (Gurnell and Petts, 2006), organic matter, nutrient (Francis *et al.*, 2009) and diaspore (O'Hare *et al.*, 2012) fluxes. By modulating matter and energy fluxes, riparian plants cause drastic modulation of fluvial landform dynamics (Gurnell *et al.*, 2012; Gurnell, 2014). They also modify the biophysicochemical properties of riparian substrates by means of roots, their interactions with bacteria (Doty *et al.*, 2005) and mycorrhizal fungi (Beauchamp *et al.*, 2006), uptake of nutrients (Pinay *et al.*, 2000) and their release of organic matter and exudates in the substrate. Furthermore, they strongly modulate local microclimatic conditions, such as air and ground surface temperature and humidity, and light regime (for a review see Tabacchi *et al.*, 2000).

The aim of this paper is to explore the role of engineer plants in modulating the four dimensions of river ecosystems within the *fluvial biogeomorphic succession* (FBS) framework proposed by Corenblit *et al.* (2007) and the abiotic and biotic interactions that result from these modulations. We stress that the four-dimensional framework needs to be reinforced by considering feedbacks between vegetation and hydrogeomorphic dynamics on both ecological (<10³ years) and evolutionary (>10⁵ years) timescales in order to obtain a better understanding of two fundamental properties of riparian ecosystems linked to system stability: resistance and resilience (*sensu* Holling, 1973, 1996; O'Neill *et al.*, 1986; Tilman, 1996). Ecosystem resistance relates here to the capacity of fluvial landforms and associated communities to maintain their structure, or a successional trajectory, during periods of disturbance caused by hydrogeomorphic factors. Ecosystem resilience refers here to the capacity of the biogeomorphic system to regain its original structure and function and thus to 'absorb' disturbances.

Based on the literature and on empirical contemporary data collected on the River Tech (Pyrenees, France), we propose an original explanation of how the hierarchy of feedbacks between vegetation and river dynamics may have led to the emergence of characteristic fluvial biogeomorphic types (FBT). Here we define these FBTs according to specific conditions of biogeomorphic resistance and resilience, and to dominant ecological strategies and plant diversity.

In the first section we provide a brief description of the *fluvial biogeomorphic succession* (FBS) model. In the second section we use palaeontological and geological evidence to document the fundamental FBS phases of river ecosystem organization from the beginning of the colonization of continents by land plants (in the Middle Ordovician) and the pattern of abiotic–biotic feedbacks related to each FBS phase. The third section presents a description of the resultant effects of

abiotic–biotic feedbacks on modern river biogeomorphic structure, resistance and resilience along the four dimensions. In the last section we propose a synthetic conceptual eco-evolutionary model of biogeomorphic organization related to the concept of niche construction proposed by Odling-Smee *et al.* (2003).

The fluvial biogeomorphic succession model: describing ecological and evolutionary feedbacks between riparian plants and fluvial geomorphology

We argue that feedbacks between plants and fluvial geomorphology on both ecological and evolutionary timescales can be conceptualized using the fluvial biogeomorphic succession (FBS) model initially proposed by Corenblit *et al.* (2007). This conceptual model, which encompasses four fundamental phases of biogeomorphic organization (i.e. geomorphic, pioneer, biogeomorphic and ecological), describes the structural and functional consequences of abiotic–biotic feedbacks on the riparian ecosystem (Figure 1).

The FBS is related to a recurrent and characteristic positive feedback of matter aggregation, stabilization and vegetation growth and succession, during which the riparian ecosystem shifts from a highly resilient state dominated by extrinsic

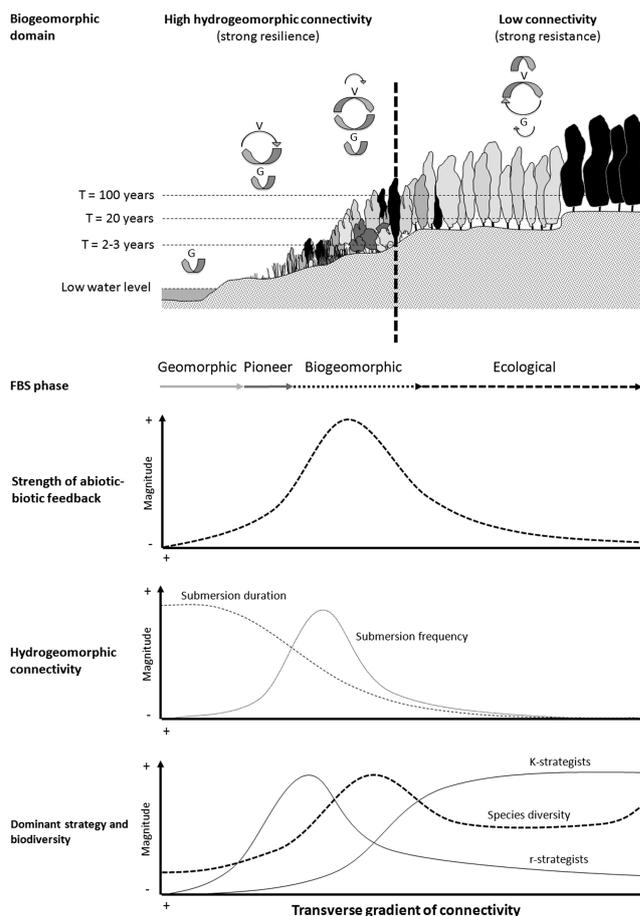


Figure 1. Model of fluvial biogeomorphic succession (FBS *sensu* Corenblit *et al.*, 2007). The FBS encompasses four main phases of biological and geomorphic organization (i.e. geomorphic, pioneer, biogeomorphic and ecological). The different phases are located in this figure along the gradients of abiotic–biotic feedback strength, hydrogeomorphic connectivity, dominant strategy and biodiversity. The strength and the modality of interaction between vegetation and geomorphology are schematized in the figure, where V = vegetation; and G = geomorphology.

hydrogeomorphic processes and r-strategist organisms to a resistant state dominated by intrinsic biological processes and K-strategist organisms (Corenblit *et al.*, 2009a; Francis *et al.*, 2009). Many studies highlighted the way this positive feedback is driven by pioneer engineer riparian trees (e.g. in the temperate climate, species of *Populus*, *Salix*, *Alnus* and *Tamarix* genera) that trap sediment, organic matter, nutrients and diaspores within active river channels (for a review see Gurnell, 2014).

The FBS model was initially defined with empirical data from the River Tech (for a full description see Corenblit *et al.*, 2007, 2009a, 2009b). Figure 2 schematizes the biogeomorphic structure and sediment dynamics along the transverse and vertical gradients of hydrogeomorphic connectivity and vegetation succession, as observed within the river's piedmont zone. Feedbacks between vegetation succession and the construction of fluvial landforms led to a reciprocal dependency between the physical environment

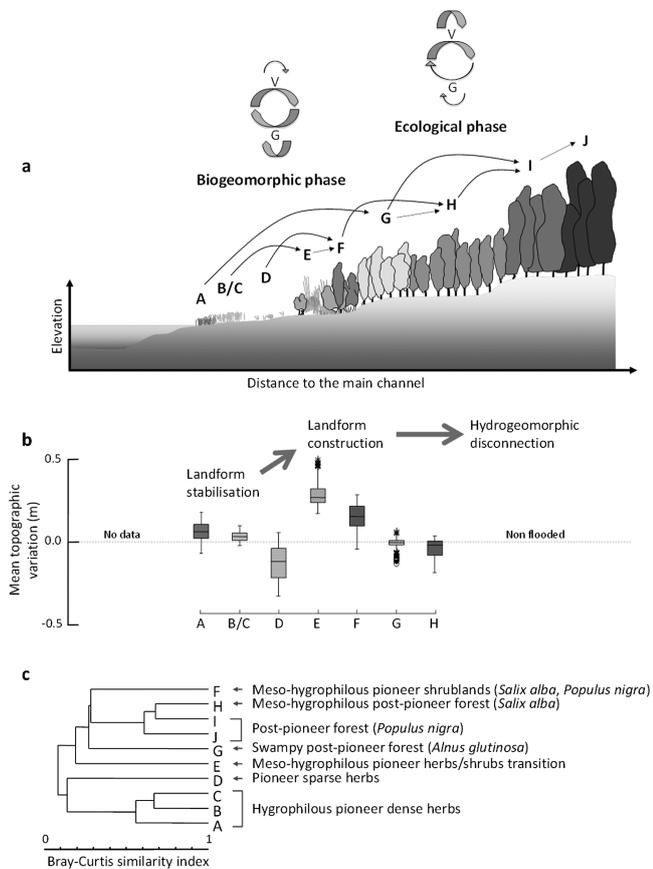


Figure 2. Illustration of the biogeomorphic succession pattern observed on the River Tech (Pyrenees, France). The biogeomorphic phase was characterized by a strong positive feedback of sediment stabilization, trapping and vegetation succession. Mean net topographic variation (recorded from 2002 to 2004 and resulting from four flood events) within vegetation types A to H are illustrated with box and whisker plots; horizontal = median; lower and upper box limits = 25th and 75th percentile; whiskers extend to the 1st and 99 Falcon-Lang percentile; circles = outliers; stars = extreme points. During the FBS, dense herbaceous mats systematically contributed to sediment stabilization while ligneous communities trapped huge quantities of sand and diaspores (b). Mean topographic changes varied significantly between the different vegetation units (one-way ANOVA with repeated measures: $P < 0.0001$). V = vegetation and G = geomorphology. Such processes of landform construction enhanced hydrogeomorphic disconnection and vegetation succession. The pattern of vegetation succession was defined using a Hierarchical Cluster Analysis with the Bray-Curtis similarity index (a and c). Succession trajectories shown in (a) were defined according to changes in the similarity matrix in the interval between 2002 and 2004. Modified from Corenblit *et al.* (2009b).

and the floristic composition which was documented using a Canonical Correspondence Analysis (Figure 3). Correlations between the hydrogeomorphic variables and the floristic composition reported in Table I suggest that vegetation succession on the River Tech follows a transverse gradient of hydrogeomorphic disconnection and a vertical (topographic) gradient of sediment grain-size fining upwards related to sediment trapping by engineer plants.

The FBS model was based on the recognition that the overall evolution of riparian vegetation would have led to the development of morphological, physiological and phenological functional traits that favoured resistance to hydraulic constraints, sediment scouring and burial. Corenblit and Steiger (2009) suggested that arising from this evolutionary path, the resistance and resilience of vegetation during and after floods may have led to major ecosystemic modifications in rivers on an evolutionary timescale. In addition to affecting on the long term fluvial geomorphology, plant functional traits would have affected riparian ecosystem resistance and resilience and resulting structure, along the biologically constructed longitudinal, transverse and vertical river dimensions.

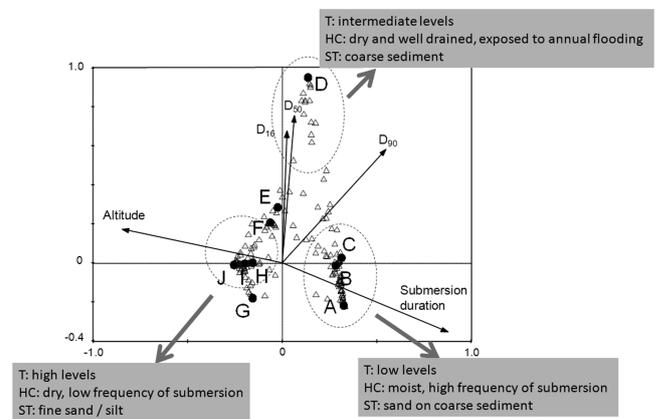


Figure 3. Canonical correspondence analysis undertaken on the River Tech floristic composition (plant species relative cover). 54% of the floristic structure was explained by the hydrogeomorphic variables modulated by engineer plants. Values indicate a very good correlation between axis 1 related to the hydrogeomorphic parameters and axis 1 related to the floristic composition ($r = 0.99$, Table II). The correlation between both axes is also very good ($r = 0.96$, Table II). The first canonical axis expresses a gradient of altitude, flood duration and D_{90} grain size. The correlation is negative with altitude height ($r = -0.84$, Table II); positive with flood duration of ($r = 0.87$, Table II); and positive with D_{90} ($r = 0.55$, Table II). The second canonical axis expresses a gradient of sediment grain size (D_{16} , D_{50} and D_{90} , Table II). The correlation is positive with the three variables (D_{50} : $r = 0.73$, D_{16} : $r = 0.65$, D_{90} : $r = 0.56$, Table II). CCA was performed with CANOCO v. 4.5.

Table I. Correlation matrix between the different parameters and between axis 1 and axis 2 of the canonical correspondence analysis (CCA) (biplot in Figure 3)

	Species (axis 1)	Species (axis 2)	Hydrogeo. (axis 1)	Hydrogeo. (axis 2)
Species (axis 1)	1.00	-0.01	0.99	0.00
Species (axis 2)	-0.01	1.00	0.00	0.96
Altitude	-0.84	0.17	-0.85	0.17
Submersion duration	0.87	-0.34	0.88	-0.36
D_{16}	0.02	0.65	0.02	0.68
D_{50}	0.06	0.73	0.06	0.75
D_{90}	0.55	0.56	0.55	0.58

Based on observations from the palaeontological and sedimentary rock records, Davies and Gibling (2013, their Figure 25) showed that it may be possible to conceptually apply the FBS, initially proposed at an ecological timescale, to an evolutionary timescale. This requires describing the hierarchy of feedbacks between vegetation evolution and fluvial geomorphic adjustments that would have existed at different intervals of the Palaeozoic Era. Such a description suggests that the ways contemporary riparian ecosystems organize along the four river dimensions can be placed within an eco-evolutionary history (*sensu* Post and Palkovacs, 2009) by considering: (i) how ancient plants responded to hydrogeomorphology; (ii) how these responses fed back on hydrogeomorphic processes and fluvial landforms; and (iii) how the geomorphologic modifications fed back on the evolutionary adaptations of vegetation and on ecosystem structure, function and stability.

Plants and geomorphology co-adjusted along the river spatial dimensions on an evolutionary timescale

Plants have colonized non-marine environments since at least the Middle Ordovician (c. 470–458 Ma). They evolved traits that improved their ability to face terrestrial constraints and more specifically to colonize different patches of the riparian environment, including diverse adaptations that increased their resistance to long periods of aqueous submersion or water deficit, intermittent burial by sediment and mechanical constraints imposed by flowing water (for a review see Bornette *et al.*, 2008). Aided by these adaptations, land plants greatly diversified between the Silurian and the Carboniferous (Niklas *et al.*, 1983) and spread within river corridors from downstream to upstream habitats and from river margins to perched floodplains and river channels, and, ultimately, to upland environments. As riparian plants progressively colonized entire river corridors, they increased their propensity to frequently and permanently modulate hydrogeomorphic processes, thus contributing to a wholesale global re-shaping of fluvial landscapes (Gibling and Davies, 2012). These modulations of hydrogeomorphic processes and fluvial landforms have occurred in all four dimensions of river systems: (i) the longitudinal dimension, related to the upstream–downstream gradient of energy from headwaters to the river mouth; (ii) the transverse dimension, related to the gradient of hydrological connectivity (in terms of the duration and frequency of plant submersion) and depending on the distance to the floodplain of a water channel; (iii) the vertical dimension, related to exchanges between groundwater and surface flows and depending on elevation above the water surface at low flow stage; and (iv) the temporal dimension, which considers state changes to the three spatial dimensions over time (Figure 4). The upstream–downstream gradient of energy needs to be considered here as a conceptual simplification of the longitudinal variation in stream power.

Based on a synthesis of field evidence, Davies and Gibling (2010a, 2010b, 2011, 2013) drew on ancient geomorphic elements interpreted from the structures and internal architecture of sedimentary strata to show how and to what extent fluvial landscapes adjusted during the c. 242 Ma interval from the start of the Cambrian to the end of the Carboniferous, with an apparent relationship between these changes and stepwise evolutionary adaptations in early terrestrial vegetation (Figures 5 and 6). The authors noted that fluvial types greatly diversified over hundreds of millions of years, particularly between the Late Silurian and Pennsylvanian, ultimately leading to the appearance of

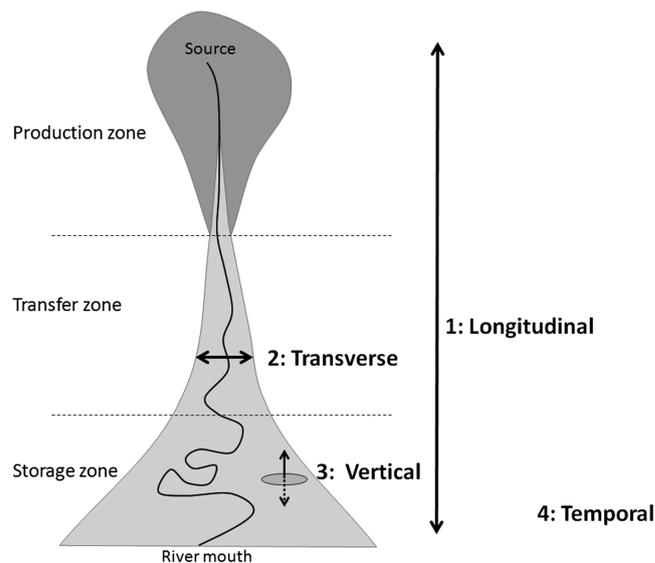


Figure 4. The four-dimensional framework. In this framework, matter and energy fluxes are considered along four river-dimensions: (1) longitudinal; (2) transverse; (3) vertical; and (4) temporal.

new *biogeomorphic types* (e.g. meandering, island braided, anastomosing; Figure 6), with niche-partitioned riparian ecosystems.

Despite the incompleteness and inherent bias of the geological record, which preserves preferentially the alluvium of downstream reaches of lowland rivers, a number of first appearances of biogeomorphic factors can be identified in the deep-time record. The following sections outline the ongoing development of rivers as Palaeozoic plants colonized the land, with the essential caveat that the apparent first appearances can only be considered the latest possible appearances, and that the factors may have been in operation even longer (though evidence for them may not be preserved, or not yet discovered, in the palaeontological record).

Before the Middle Ordovician: fluvial dynamics driven solely by physical processes

Land plants (embryophytes) have colonized non-marine environments since at least the Middle Ordovician (Taylor and Strother, 2008; Kenrick *et al.*, 2012). Before the evolution of a terrestrial flora, fluvial landforms adjusted only to geological, geomorphic and hydrological influences, with some potential analogy to ancient fluvial landforms imaged on extraterrestrial bodies such as Mars (Grotzinger *et al.*, 2011). Geomorphic adjustments were controlled by the interaction of factors associated with landscape roughness, cohesiveness, surface slope and discharge. Landscape roughness and cohesiveness are defined by factors such as bedrock properties, sediment grain size, topography, and local factors that include cohesive permafrost or clays, whereas surface slope factors govern the hydraulic geometry of the channel and its discharge. In its broadest sense, the balance between these factors remains the single most fundamental control on fluvial planform (Lazarus and Constantine, 2013). However, the ubiquitous presence of vegetation in contemporary rivers has so significantly and pervasively amplified the contributing factors to landscape roughness and cohesion that modern fluvial systems are not comparable with the truly vegetation-free systems that operated before the Middle Ordovician.

Schumm (1968) and Cotter (1978) early suggested that braided rivers would have dominated fluvial types before the greening of continents by plants. Fuller (1985) and Miall (1996) also suspected that river channel patterns have adjusted

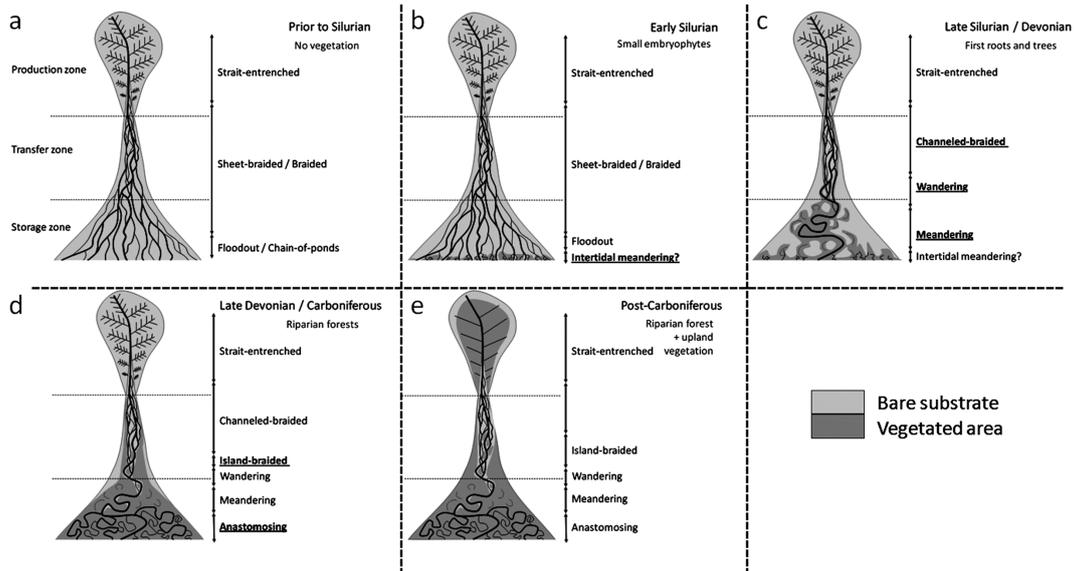


Figure 5. Schematic representation of vegetation propagation within the fluvial system from the Early Silurian to present. The emergence of new biogeomorphic types and sub-types is underlined.

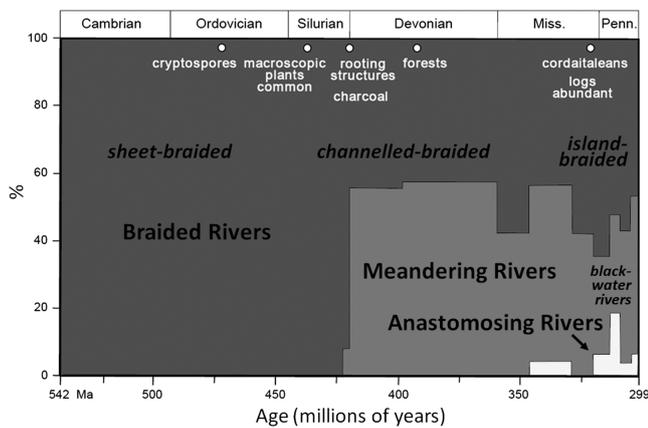


Figure 6. Evolution of the relative percentage of fluvial types from the Cambrian to the Carboniferous. Major aspects of plant evolution are indicated in the figure. Modified from Figure 1 of Gibling *et al.* (2013).

their morphology and dynamics over geological time in relation to the evolution of plants. Further research suggests that only the *geomorphic phase* of the FBS existed before the Silurian. Rivers were broadly dominated all along the longitudinal dimension by bedload transport between unconsolidated banks, and by wide and shallow channels with low topographic relief at the channel margins; permanent muddy floodplains were probably lacking (Gibling and Davies, 2012). Rivers from this time were fundamentally unstable and widened rapidly and increased the number of internal braided channels during individual precipitation events. Sheet-braided fluvial types thus widely dominated river landscapes during this period, likely from piedmont zones to the coast and across all climatic and latitudinal zones (Davies *et al.*, 2011; Long, 2011) (Figures 5(a) and 6). Sedimentological evidence shows that alluvial-fan deposits from the Cambro-Ordovician incorporate only low quantities of muddy sediments, suggesting that weathering processes were weak within river basins due to the absence of plants (Went, 2005).

Silurian: first generations of plant adaptations to terrestrial and fluvial conditions

During the Late Ordovician and Early Silurian, primitive small and poorly anchored land plants, adapting to terrestrial

conditions for the first time in Earth history, may not have significantly affected hydrogeomorphic processes (i.e. water flow and coarse sediment transport), beyond increasing local micro-landscape roughness and beginning to promote the retention of fine-grained sediment in continental environments (Davies and Gibling, 2010). However, this FBS *pioneer phase* of the terrestrialization process remains fundamental because the adaptive responses of land plants to subaerial conditions and to the fluvial environment permitted them to spread efficiently from coastal zones along the longitudinal and transverse dimensions of river corridors, affecting hydrogeomorphic processes as the reach of their habitats advanced into the continental interiors (Figure 5(b)).

Before this greening of the continents, microbial life, and probably lichens, were already contributing to the formation of primitive soils enriched with Fe and P (Raven, 1995; Taylor *et al.*, 1995). They may also have stabilized surfaces sufficiently for biochemical weathering to be enhanced (Dott, 2003; Kennedy *et al.*, 2006). As pointed out by Phillips (2009) and Viles (2012), rock weathering by micro-organisms is a precursor of sediment removal. Phillips (2009) suggested that the energy necessary to sustain rock weathering far exceeds that required for sediment erosion and transport. Thus, the Silurian represents a fundamental geological period when the biosphere could begin storing and using energy for performing geomorphic work on continental surfaces. This energy then was also progressively transferred through trophic networks that permitted geomorphic work to be accomplished by different taxa and in different ways (Naylor *et al.*, 2002; Corenblit *et al.*, 2011).

The processes leading to soil formation would have been crucial for the colonization of the continents by the first land plants. Land plants needed to develop specific anatomical structures for transporting water and nutrients from the substrate to their above-ground parts, overcoming desiccation and mechanical constraints imposed by gravity, and reproducing out of water (Kenrick and Crane, 1997; Niklas, 1997; Willis and McElwain, 2002; Gensel, 2008). Resulting adaptations included the development of mechanical supports and rhizomes (Niklas, 1997). Coastal and fluvial environments are ecologically disturbed and become frequently immersed and submerged. These restrictive environments, with strong selection pressures, were almost certainly first colonized by small,

fast-growing plants, originating from green algae (Lewis and McCourt, 2004), and which probably had high mutation rates. Because non-marine environments were unoccupied, the adaptive walks of the first land plants through the morphospace (i.e. fitness landscape) were mainly defined by physical and chemical factors (Niklas, 1997). From the end of the Ordovician to the mid-Silurian small vascular tracheophyte genera, such as *Cooksonia*, *Rhynia*, *Baragwanathia* and *Zosterophyllum*, diversified and colonized coastal zones as well as lake and river margins (Greb *et al.*, 2006). Plants of bryophyte grade probably played a significant role in rock weathering during this period (Lenton *et al.*, 2012).

Even though pioneer land plants from this interval were small and poorly anchored embryophytes (Gensel and Andrews, 1987), and thus did not contribute to controlling coarse bedload transport, these first land colonizers, especially those of tracheophyte grade with vascular tissue, started to modify river geomorphology along channels at the river mouth. The retention of muddy sediments within those vegetation patches probably permitted the first generations of small tidally-influenced meandering side-channels confined by muddy banks in the downstream reaches of lowland rivers (Figure 5(b)).

During the Late Silurian, vascular plants with more efficient supporting structures continued to develop and silt and became prominent on basin-margin alluvial fans and in alluvial deposits along the coastal zone. Probable rooting structures are known from many Early Devonian localities and may also be present in Late Silurian strata (Hillier *et al.*, 2008; Kennedy *et al.*, 2012). Plants promoted the leaching of nutrients and eutrophication of rivers (Lenton, 2001). Such enhancement in nutrient availability in river corridors may have caused an upstream–downstream eutrophication gradient during the Silurian, increasingly promoting phytoplankton blooms, carbon and nitrogen fluxes and anoxia from upstream to downstream within lowland plains, as Algeo *et al.* (1995) and Algeo and Scheckler (1998) documented based on the Devonian marine record. In relation to the production of mud through the interaction between vegetation and the substrate, muddy floodplains started to develop in lowland plains during the Late Silurian. At the same time channelled-braided rivers (comprising more moderated, narrow and stable braided channel features akin to those seen in modern braided streams) started replacing the increasingly rare sheet-braided type in lowland plains (Davies *et al.*, 2011) (Figures 5(c) and 6). Vegetation cover increased dramatically in the latest Silurian, paving the way for the Early Devonian appearance of the first riparian woody vegetation (Gerrienne *et al.*, 2011). At the close of the Silurian, rivers with single-thread meandering trunk channels, stabilized in part by the increasing number of cohesive muddy floodplains and perhaps locally by organic structures, started to develop (Davies and Gibling, 2010b).

Devonian: strong abiotic–biotic feedbacks

During the Devonian, the evolution of wood and riparian forests drastically changed river landscapes through increased bank cohesion, surface roughness, and fine-grained sediment supply. Vegetation increased in abundance, diversified greatly and evolved toward lignified shrub, bush and arborescent morphologies (Driese *et al.*, 1997; Elick *et al.*, 1998; Driese *et al.*, 2000; Meyer-Berthaud *et al.*, 2010; Meyer-Berthaud and Decombeix, 2012; Stein *et al.*, 2012; Kennedy *et al.*, 2013). Storage of plant organic matter in soil increased during this period because of the development of aerial and underground vegetation biomass and the appearance of lignin resistant to decomposition (Gensel *et al.*, 2001). Lignin-bearing plants that colonized lowland wetlands, such as *Lepidodendron* (Taylor and Taylor, 1993) and the progymnosperm *Archaeopteris* (Meyer-Berthaud *et al.*, 1999), developed morphological and

physiological traits that increased their resistance to long-term submersion, turbidity and fine-sediment burial (e.g. arborescence, adventitious roots, tolerance to anoxia). Many types of rooting system developed during this period, some of them well ramified and attaining more than 1 m depth. The deep rooting system of plants such as *Archaeopteris* (probably >4 m) also would have favoured their propagation on floodplains beyond the immediate river margins during the Devonian (Algeo and Scheckler, 1998).

By the Middle to Late Devonian, lowland plains were covered by dense riparian forests in river corridors with different strata and dominated by tall trees with different kinds of large and deep rooting (Bockelie, 1994). The Gilboa riparian forest documented by Stein *et al.* (2007, 2012) represents a famous example encompassing an overstory stratum dominated by the progymnosperm *Archaeopteris* and an understory stratum dominated by the fern-like *Rhacophyton*. Such diversification of plant physiognomy can be related to the fact that taller plants obtain better access to light and to wind for spore dispersion (Niklas, 1997). Large size and morphological features of lycopods, arborescent horsetails, progymnosperms and seed ferns thus provided an optimization of light interception, mechanical support and spore dispersal and production (Niklas, 1997). However, such attributes provide a selective advantage mostly in a stable environment. Thus, such traits could have developed through a fundamental moderating feedback between plant engineering and fluvial geomorphology, seemingly common during the Devonian (Gibling and Davies, 2012).

The increase in the mechanical and physiological resistance of vegetation to prolonged submersion or water-deficit stress led during this FBS *biogeomorphic phase* to drastic geomorphic changes in river systems through the concomitant stabilization of river channels and the construction of floodplains. Tree roots greatly contributed to stabilization of river banks and concentration of flow within a single channel with a decreased width/depth ratio. Aerial structures increased surface roughness at the river margin and on the floodplain, leading to fine-sediment retention and raised floodplains. Rooted plants colonized laterally-accreting alluvial point bars and banks, contributing to their stabilization and promoting at the same time fine-sediment trapping and retention in specific locations within rivers' active tracts (Davies and Gibling, 2010b). As suggested by Braudrick *et al.* (2009), a self-sustaining free meandering style only exists in conditions where the bank strength is greater than that of deposited bedload and where large amounts of fine suspended sediment can be deposited and preserved on the migrating point bar. Devonian vegetation thus promoted the development of meandering rivers (Figures 5 (c), (d) and 6) dominated by lateral accretion, systematic lateral channel migration, and chute and neck cutoffs (Cotter, 1978; Davies and Gibling, 2010b).

In part due to these biogeomorphic feedbacks between vegetation evolution and geomorphology, by the Middle Devonian riparian ecosystems began to be partitioned along the longitudinal, transverse and vertical dimensions. Such floristic contrasts were a response to the diversification of conditions for submersion frequency and duration, sediment erosion/deposition and nutrient availability (Allen and Gastaldo, 2006). This floristic and geomorphic partitioning certainly involved a strong feedback between engineer plants affecting water flow, sedimentation and landforms and their evolutionary trajectory. This eco-evolutionary feedback was enhanced through the construction of muddy and aggraded floodplains and may have promoted the evolution of certain plant species, such as *Archaeopteris*, toward better competitive capacities and tolerance to drier conditions and seasonality (Meyer-Berthaud *et al.*, 1999; Stein *et al.*, 2007, 2012). The

development of the arborescent physiognomy and resultant large canopies also would have reinforced ecological partitioning through changes in soil habitat (pedogenesis) and surface conditions (control of light intensity, humidity and temperature). As illustrated by the Gilboa forest (Stein *et al.*, 2007, 2012), the new Middle Devonian ecological niches led to a great increase in floristic and faunal biodiversity and ecological strategies, linked to feedbacks between biotic and abiotic processes (Gibling and Davies, 2012). Some Devonian plants may have been capable of colonizing upland areas (Decombeix *et al.*, 2011).

Carboniferous: culmination of non-marine biogeomorphic ecosystems

During the Carboniferous rivers attained the FBS *ecological phase*. Muddy aggraded floodplains were well developed and riparian ecosystems encompassing a diverse array of plants and faunal species already existed (Willis and McElwain, 2002; Greb *et al.*, 2006). Biotic interactions such as competition may have become preeminent selection pressures defining the structure and function of the riparian ecosystem at the scale of the entire river corridor within lowland plains and piedmont zones (Figure 5(d)).

At the end of the Devonian and through the Carboniferous, a major turnover and diversification of riparian vegetation took place. By this time, the main vegetational traits of response to hydrogeomorphology and influence on hydrogeomorphic conditions already existed. Tall trees such as *Calamites* and *Psaronius* developed (Willis and McElwain, 2002). Riparian plants continued adapting to water stress, and certain species colonized drier raised levees within the alluvial plain (Falcon-Lang and Galtier, 2010). At the end of the Mississippian, gymnosperms developed deep rooting systems at least 4 m below the surface and colonized the driest, well drained areas of the alluvial plains (DiMichele *et al.*, 2010). Most contemporary types of rooting had evolved by the end of the Carboniferous (Pfefferkorn and Fuchs, 1991) and, of particular importance, was the evolution of root systems that promoted high shear strength and resistance to erosion (DiMichele *et al.*, 2010). The development of the seed habit also permitted trees to colonize drier levees and expand into upstream valleys (Algeo and Scheckler, 1998) and, in very dry lowland areas, even into coastal sabkhas (Falcon-Lang *et al.*, 2011). Wetland vegetation reorganized during the Moscovian–Kasimovian transition according to a global increase of aridity. Wetlands were fragmented and further partitioned, and riparian plants adapted further to drier and seasonal conditions (DiMichele *et al.*, 2009). Woody cordaitaleans and conifers dominated drier Carboniferous episodes, forming dense forested patches in inland settings (Falcon-Lang *et al.*, 2011; Bashforth *et al.*, 2014).

Another important adaptation during the Pennsylvanian was the ability of certain plants to resist more efficiently mechanical constraints imposed by water flow during floods and thus to grow directly within river channels (Fielding and Alexander, 2001; Fielding *et al.*, 2009). Biomechanical traits promoting this habit include a high resistance to breakage and flexibility of roots and aerial structures that permitted plants to modulate the geomorphic setting in the most active zones of the river corridor. For example, calamitalean sphenopsids were adapted to hydrogeomorphic disturbance and sediment burial, with diverse propagation modes and the possibility of clonal growth after breakage (Gastaldo, 1992; Pfefferkorn *et al.*, 2001; Allen and Gastaldo, 2006). Such plants may have spread upstream along the energy gradient, and consequently may have contributed to the modulation of fluvial landforms directly from inside river channels along both longitudinal and transverse river dimensions.

By the end of the Carboniferous, the full range of the most abundant fluvial biogeomorphic types seen on the Earth surface today had evolved (Davies and Gibling, 2013). The great expansion of riparian forests along longitudinal, transverse and vertical river gradients, which occurred during the Carboniferous, led to a large increase in substrate cohesion and landscape roughness, and thus to storage of fine sediment and organic matter, at the scale of the entire fluvial corridor.

Vegetation thus drastically modified fluvial landform dynamics within lowland-plain reaches with low to medium energy. By the Early Pennsylvanian, the widespread global development of anastomosing rivers and the appearance of blackwater rivers (Figures 5(e) and 6) with single or multiple fixed channels filled with sand resulted in stable aggrading muddy floodplains, which acted as important sinks for fluvial sediment, organic matter and nutrients transported from the river channel to the adjacent floodplains (Davies and Gibling, 2011). Davies and Gibling (2011, 2013) suggested that this threshold-crossing change in fluvial geomorphology during the Mississippian was promoted by several factors. These included the increasing arborescence and density of vegetation which developed diverse root systems, the possibility for vegetation to grow directly in active channels and on above-water-table floodplain levees on dryland plains, and the increased supply of large woody debris, promoting log jams and avulsive behaviour within rivers.

In the late Carboniferous, vegetation colonized upland valleys and probably started to spread within upland areas (Falcon-Lang and Bashforth, 2005; Gibling *et al.*, 2010). Phillips and Lorz (2008) and Pawlik (2013) highlighted the ways in which vegetation can affect upland rocks through weathering, pedogenesis, and the regulation of mineral and organic matter transfer from hillslopes to river channels. At this time vegetation growing along banks and within the active channel would have started to interact more intensively with coarse bedload. The increase in the supply of large woody debris to river channels in the piedmont zones would have favoured also the development of new biogeomorphic types related to avulsion dynamics promoted by accreting pioneer vegetated points or log jams. By promoting avulsions, pioneer vegetation growing directly in river channels and accumulations of large woody debris contributed to the Pennsylvanian appearance of wandering and island-braided types (Gibling *et al.*, 2010; Ielpi *et al.*, 2014) (Figures 5(e) and 6). As pointed out by Tockner *et al.* (2003) and Gurnell *et al.* (2005), these biogeomorphic types are characterized by a mosaic of habitats within a large active channel. In particular, riparian islands initialized by pioneer vegetation or log jams often constitute >50% of the active corridor. Pioneer islands contribute in creating points of matter aggregation, and vegetation grows within a highly dynamic active tract (Gurnell *et al.*, 2001; Francis *et al.*, 2009). Church (2002) suggested that wandering and island-braided types are a potentially persistent state marking the transition between braided and meandering types, characterized by strong feedback dynamics between biota and abiotic elements (Francis *et al.*, 2009).

Palaeontological evidence from the Pennsylvanian indicates that the biogeomorphic partitioning of the riparian ecosystem was important at this time, with trees specialized to different levels of hydrogeomorphic connectivity (Bashforth *et al.*, 2011). For example, the lycopsid tree *Sigillaria* may have preferred partly disconnected habitats with periodic substrate dryness whereas calamitalean trees, exhibiting a clonal rhizomatous growth, were adapted to moist disturbed areas and could easily recover from sediment burial (Gastaldo, 1992). The spatial biogeomorphic partitioning which occurred during the Pennsylvanian can be linked with biogeomorphic

succession dynamics (*sensu* Corenblit *et al.*, 2007). This period exhibits the earliest palaeontological evidence for riparian succession associated with fluvial landform construction. Smith (1962) noted vertical changes in spore content suggesting that plant succession and vertical changes in substrate properties took place in parallel and indicating temporal succession of riparian habitat conditions (see also Greb *et al.*, 2002). During this interval, competition between riparian tree species may have become an important selection pressure within aggraded and stabilized floodplain levees. Competition between riparian tree species and tree species spreading from uplands into the floodplain margins also may have imposed new selection pressures. These selection pressures may have favoured the development of K-traits such as increased height with developed canopies for accessing light, deep roots for accessing water, and as reported by Chaloner and Sheerin (1981) an increase in the size and quality of seeds.

The widespread engineering of fluvial systems by new and diverse plant communities also promoted the creation of new niches for a variety of newly evolved fauna. The major Palaeozoic diversifications in fluvial style (namely at the Silurian–Devonian and Mississippian–Pennsylvanian boundaries) closely correspond with major expansions in terrestrial faunal biodiversity (Davies and Gibling, 2013).

Post-Palaeozoic: toward a global spread on continents by seed plants

Following the Carboniferous, a major innovation directly related to seed habit was the ability of plants to spread on upland surfaces (Figure 5(e)). Seed plants became dominant during the Permian. By the Upper Permian, more than 60% of the Earth's known flora was composed of gymnosperm species, which spread globally on continents and exhibited palaeogeographic partitioning from low to high latitudes and from wet to dry and warm to cold biomes. These Permian biomes fluctuated in space according to global climatic and tectonic changes, particularly as the assembly of the global supercontinent Pangea resulted in a worldwide increase in aridity, slowly spreading from present-day North America, through Europe, and into Asia as the Permian progressed (Greb *et al.*, 2006). Many Permian river systems are likely to have been significantly influenced by this global aridity and its associated reduction of global vegetation cover (e.g. an increase in braided river planforms).

After the Palaeozoic, other major innovations in vegetation arose, though the precise effects of these on the eco-evolutionary history of rivers is less well studied. One major Mesozoic innovation was the Cretaceous rise of angiosperms (flowering plants). Angiosperms, comprising diverse kinds of trees, shrubs and herbs, have dominated the majority of terrestrial habitats since at least the earliest Paleocene. The ancestors of angiosperms were probably herbaceous weedy shrubs with a rapid life cycle (Crane, 1987; Friis *et al.*, 1999, 2001). Based on a molecular study, Qui *et al.* (1999) suggested that the basal group of angiosperms is Nymphaeales, which are aquatic rhizomatous herbs. The Cenozoic also saw a major evolutionary step in the history of vegetation, with the rise and spread of grasses, which may also have first evolved in the latest Mesozoic (Greb *et al.*, 2006). The effect of the rise of grasses on river morphology during this period has yet to be studied and represents a future challenge.

During the Quaternary, huge climatic fluctuations also modulated the spatial distribution of biogeomorphic types, leading to fluvial metamorphosis as documented mainly in the northern hemisphere (Baker and Penteado-Orellana, 1977). For example, it was shown that the spatial pattern of *Populus* spp. (e.g. *P. nigra* L.), which are keystone ecosystem engineers within temperate rivers (Gurnell and Petts, 2006),

fluctuated during the Quaternary according to ice ages (Bennett *et al.*, 1991). Cottrell *et al.* (2005) showed that populations of *P. nigra* remained during the last ice age in southern parts of the European continent. *P. nigra* succeeded in recolonizing north and central European fluvial corridors during the last 10 000 years.

Although the repartition of the different biogeomorphic types around the world varied greatly according to geological, climatic and anthropogenic changes, the potentially available biogeomorphic types, which emerged from the late Silurian to the Carboniferous, remained the same.

Effects of today's plant traits on biogeomorphic structure and stability along the river dimensions

We argue that modern riparian landscape dynamics and the way in which related aquatic and riparian plant, animal and micro-organism communities organize reflects millions of years of engineering by vegetation. It is the ligneous angiosperms, originating in the Mesozoic and evolving toward extant herbs, riparian shrubs and trees, that currently most drastically affect hydrogeomorphic parameters and river morphology along the longitudinal, transverse and vertical dimensions of the river corridor (Corenblit *et al.*, 2014; Gurnell, 2014).

Many phenological, physiological, morphological and biomechanical traits of contemporary riparian angiosperms are specifically related to river patterns and processes (Lytle, 2001; Karrenberg *et al.*, 2002; Lytle and Poff, 2004; Bornette *et al.*, 2008; Puijalon *et al.*, 2011). The successive adaptations improved the resistance and resilience of contemporary riparian plants within the naturally disturbed fluvial environment and thus increased their capacity to modulate their geomorphic environment during floods (Gurnell, 2014). Modern plant response traits that improve tolerance to long-term submersion and sediment burial include height, floatability, and production of adventitious roots, and these traits are preferentially selected within downstream low-energy river sections with cumulatively more discharge and turbidity (Naiman and Décamps, 1997; Karrenberg *et al.*, 2002; Lytle and Poff, 2004). Additional plant traits improve mechanical resistance (i.e. tolerance or avoidance) to breakage and uprooting, including a small to intermediate size, flexible stems, breaking points and deep rooting (Beismann *et al.*, 2000). Adaptations to fluvial disturbance that reinforce vegetation resilience include for example the ability to reach sexual maturity over a short period, production of numerous buoyant seeds, capability to resprout, and adequate timing of seed production according to the natural flow regime (Mahoney and Rood, 1998). Such additional response traits were selected within more energetic intermediate to upstream bedload river sections.

Plant traits modify fluvial types and related biogeomorphic resistance and resilience

In modern rivers, as a result of the ability of vegetation through physiological or mechanical adaptations to resist hydraulic constraints and colonize bare alluvial surfaces between large infrequent floods, fluvial landforms increase in relative elevation, the percentage of fine-sediment and organic matter content and their resistance to erosion (Bertoldi *et al.*, 2011a; Gurnell, 2014). Taking into account the key role of vegetation traits in modern river geomorphology, *fluvial biogeomorphic types* (FBT) may be considered as the second of two overall *fluvial types*. The first type is mineral-dominated and riparian vegetation does not significantly control the geomorphology, while the second is the *fluvial biogeomorphic type* in which

riparian vegetation largely and durably modulates or controls channel and floodplain geomorphology. Brunsden and Thornes (1979) transient form ratios (TFr) can be used here for distinguishing the two categories through estimating the range of action of engineer plants within a fluvial corridor (Equation (1)) (Phillips, 1999; Corenblit *et al.*, 2011; Jones, 2012; Eichel *et al.*, 2013).

$$\text{TFr} = F/D \quad (1)$$

where F represents the time needed for the biogeomorphic structure to be formed (i.e. relaxation time related to vegetation dispersal, recruitment and establishment traits); and D represent the recurrence interval of destructive floods at the scale of the corridor. The transient form ratios of the rate of landform construction by engineer plants (F) and the rate of destruction by water flow (D) must be <1 or at least =1 to meet the criterion of a FBT.

These two types may be subdivided into several subcategories according to the geological and bioclimatic setting. However, within temperate and tropical biomes two main categories of mineral-dominated fluvial types can be identified in upstream sections in which hydraulic forces exceed the resistance capabilities of plants: straight-entrenched (SE) in torrential production zones, and braided (B) in transfer zones (Table II). Hyper-arid, polar and bedrock rivers also form categories of mineral-dominated fluvial type. Four categories of contrasted fluvial biogeomorphic types exist within rivers, each with characteristic modulations of the balance between cohesive and destructive forces: island-braided (IB), wandering (W), meandering (M), and anastomosing (A) (Table II). Several functions such as sediment, nutrient and organic-matter retention and transformation are modulated differently according to the biogeomorphic type. Specific spatiotemporal modulations of hydrogeomorphic stress and disturbance and biotic interactions and diversity are also related to each biogeomorphic type and to each eco-region (Gurnell, 2014).

Thresholds in fluvial landform remobilization related to FBTs do not solely depend on topography, intrinsic sediment cohesiveness and flood magnitude and frequency, as was the case before the colonization of continents by plants. As pointed out by Gurnell (2014), fluvial landform erosion or removal thresholds are strongly modulated by vegetation resistance traits to hydrodynamic forces. Owing to stabilization by roots, fluvial landforms are more resistant to erosion during floods. They are also resilient between large infrequent destructive floods where the rate of vegetation growth and related engineer effects exceeds the frequency of destructive floods (Francis *et al.*, 2009; Corenblit *et al.*, 2010; Bertoldi *et al.*, 2011b). As suggested by Corenblit *et al.* (2007, 2011) and Gurnell *et al.* (2012), along the longitudinal dimension, the strength of abiotic–biotic feedbacks leading to an increase of biogeomorphic resistance and resilience reaches its maximum within rivers at intermediate levels of hydrogeomorphic disturbance, mainly in meandering, wandering and island-braided sections with low to high stream power (approximately 10 to 300 W m^{-2}) (Table II).

Biogeomorphic feedbacks in these sections can under certain circumstances lead to changes in fluvial pattern often interpreted in fluvial geomorphology as ‘fluvial metamorphoses’ (Schumm and Lichty, 1963; Schumm, 1969; Gurnell and Petts, 2002; Tal and Paola, 2010). In the landscape these changes are represented by systems changing toward: (i) biogeomorphic types dominated by sediment deposition and vegetation succession (e.g. meandering type); or (ii) biogeomorphic types dominated by erosion and vegetation rejuvenation (e.g. island-braided type). Wandering types may

represent transient patchy metastable states marking a possible progressive or abrupt transition between the two alternative states. The different biogeomorphic types represent a combination of variations in discharge and sediment load, and are related to the thresholds of vegetation resistance to floods or stress (e.g. drought), to their resilience, and to their landform construction effects (i.e. their effect and response functional traits).

A scale-dependent feedback controls the repartition of constructive and destructive forces within the fluvial corridor. Levin and Segel (1985) pointed out that self-organized spatial patterns originate at the scale of the landscape in diverse environments from scale-dependent interactions between physical processes and biota (for a full description of the process see Rietkerk and Van de Koppel, 2008). Scale-dependent feedbacks occur within ecosystems when the landscape pattern initially based on key physicochemical variables is reinforced and maintained by a positive feedback due to plant resource acquisition at the local scale (in-site short range activation) and when an inhibiting feedback occurs at a larger scale (off-site long range inhibition). Recent studies suggest that within instable and disturbed land–water interface ecosystems (e.g. saltmarshes, coastal dunes, rivers) the combination of and balance between local in-site protective and accretive effects of engineer plants and their off-site erosive effects control biogeomorphic organization at the landscape scale (Gurnell *et al.*, 2005; Temmerman *et al.*, 2007; Murray *et al.*, 2008; Van Wesenbeeck *et al.*, 2008; Francis *et al.*, 2009). In a flume experiment, Bouma *et al.* (2013) showed that the spatial pattern of sediment erosion and deposition varies according to the specific morphological and biomechanical functional traits of engineer plant species. Such fundamental present-day abiotic–biotic interactions that drive landscape dynamics would not have been as prevalent in ancient environments before or early in the evolution of land plants (Davies and Gibling, 2013).

Francis *et al.* (2009) suggested that scale-dependent feedbacks between vegetation growth and hydrogeomorphic processes in fluvial corridors produce characteristic landscape structures (e.g. fluvial islands) and patterns (i.e. biogeomorphic types) along the energy gradient (see also Corenblit *et al.*, 2009b) (Figure 7(a)). Francis *et al.* suggested that short-range activation observed within and downstream of pioneer vegetation patches and long-range inhibition occurring around vegetation patches are the basic principles of fluvial biogeomorphic succession and landscape organization within flood-disturbed corridors (Figure 7(b)).

We argue that, once established, pioneer riparian plants with a sufficient anchorage and aerial biomass interact with water and sediment flow and enhance a short-range positive feedback of accumulation of fine sediment, organic matter, nutrients and diaspores within or immediately downstream from vegetation individuals and patches (Gurnell *et al.*, 2005; Corenblit *et al.*, 2009b; Francis *et al.*, 2009). The cumulative local improvement of habitat conditions for vegetation and landform stabilization within pioneer islands or on accreting point bars in turn favours organic matter production, retention and nutrient consumption by plant communities. Vegetation growth is accompanied in time by a succession of different categories of plant species (Figure 1). This self-reinforcing process of landform construction and associated vegetation succession during the FBS is regulated through the progressive disconnection of laterally and vertically accreting fluvial islands and floodplain levees from hydrogeomorphic disturbances (Bendix and Hupp, 2000; Corenblit *et al.*, 2009b).

The spatiotemporal intensity and repartition of short-range activation and long-range inhibition along the longitudinal

Table II. Description of the main fluvial and biogeomorphic types. F/D ratio: F = rate of landform formation; D = rate of landform destruction (see Corenblit *et al.*, 2011; Jones (2012))

Biogeomorphic type / *fluvial type	Description	Specific stream power range (W/m^2)	Width/depth ratio	Sediment dynamics	Vegetation control on fluvial morphology	Landform/succession turnover	F/D ratio	Dominant plant adaptation	Dominant plant strategy within the fluvial corridor
*Straight-entrenched (SE)	Straight Steep channel directly connected to hillslopes.	>300	Very low <10	Bedload	Bank stabilization	<1 year	>1	Size	r
*Braided (B)	Multiple unstable channels separated by instable bars; shaped mainly by physical processes.	>300	High >40	Bedload	Negligible	<1 year	>1	Size	r
Island-braided (IB)	Braided rivers with vegetated islands storing fine sediment, nutrients and organic matter; very high habitat turnover enhancing high landscape heterogeneity.	100–300	High >40	Bedload / mixed load	Intermediate	Few to 15–20 years	>= 1	Size/biomechanical	r
Wandering (W)	Transition between island-braided and meandering styles; characterized by growing vegetated islands frequently connecting and disconnecting from the floodplain according to active channel avulsion dynamics; high habitat turnover maintaining high landscape heterogeneity.	30–100	Intermediate 30–40	Bedload / mixed load	Intermediate	Few to 30–40 years	≈1	Size/biomechanical	r/K
Sinuuous/meandering (M)	Single channel rivers more or less sinuous; regular channel lateral migration; control of point-bar accretion and channel migration by vegetation; meander loops generally form neck- or chute cut-offs at the origin of oxbows.	10–30	Low 10–40	Suspended load	Strong	40–80 years	<1	Size/biomechanical/physiological	K

K
 Physiological
 <1
 >80 years
 Predominant
 Suspended load
 Very low <10
 <10
 Anastomosing (A)

Rivers with stable multiple fixed channels separated by aggrading and densely vegetated islands; frequent avulsions lead to the creation of secondary channels and oxbows; vegetation contributes to stabilizing river banks and trapping fine sediment during large floods.

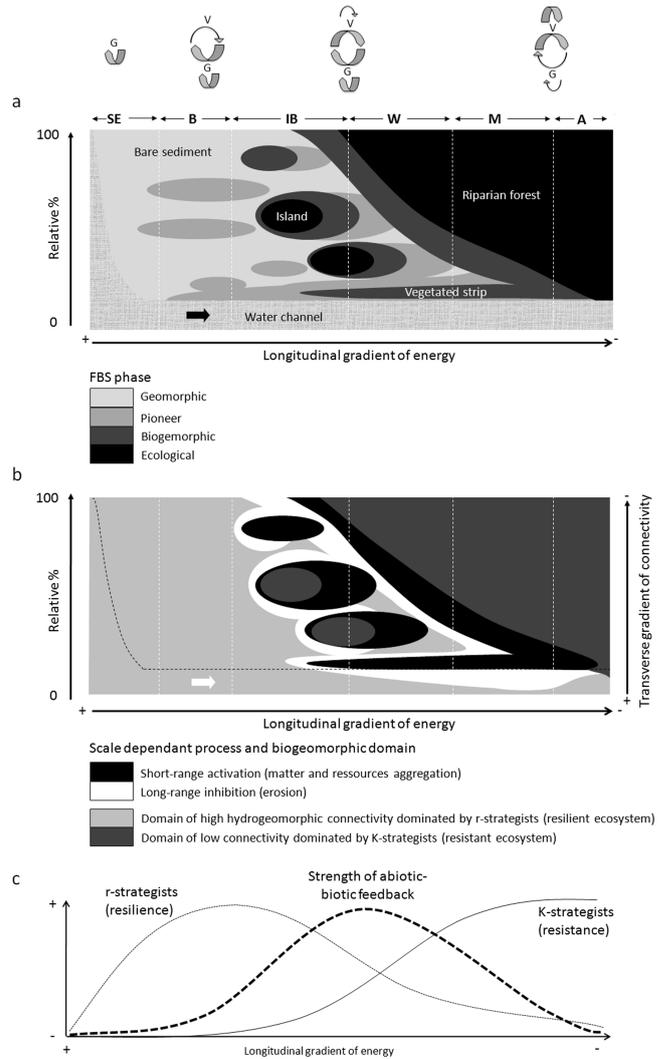


Figure 7. Conceptual model of scale-dependent feedback leading to the emergence of biogeomorphic types related to short-range activation and long-range inhibition: (a) relative percentage of the different biogeomorphic phases along the longitudinal (gradient of energy) and transverse (gradient of hydrogeomorphic connectivity) dimensions; (b) relative percentage of short-range activation and long-range inhibition along the longitudinal (gradient of energy) and transverse (gradient of hydrogeomorphic connectivity) dimensions; (c) changes in strength of abiotic–biotic feedback and related plant strategy along the longitudinal gradient. V = vegetation; and G = geomorphology. Inspired from Gurnell *et al.* (2012).

energy gradient defines the biogeomorphic type, with a characteristic patchy fluvial landscape in river sections with an intermediate level of disturbance (Figures 7 and 8). Highly energetic, straight-entrenched and braided types lack short-range activation because vegetation that acts as dissipative structure does not persist within these highly disturbed systems (Figures 7 and 8; Table II). The island-braided and wandering types exhibit a shifting mosaic of activation zones (i.e. islands of fertility) corresponding to accreting pioneer islands and floodplain levees, with inhibition zones located around pioneer islands and at the margins of floodplain levees (Figures 7 and 8; Table II). The high landscape and topographic complexity of these types contributes to high habitat and species diversity and turnover within the fluvial corridor (Ward and Stanford, 1983; Amoros and Bornette, 2002; Tockner *et al.*, 2003; Gurnell *et al.*, 2005, 2009). The single free meandering type is characterized by a concentration of the short-range activation zone on migrating point bars where pioneer riparian vegetation established, traps sediment and progressively builds

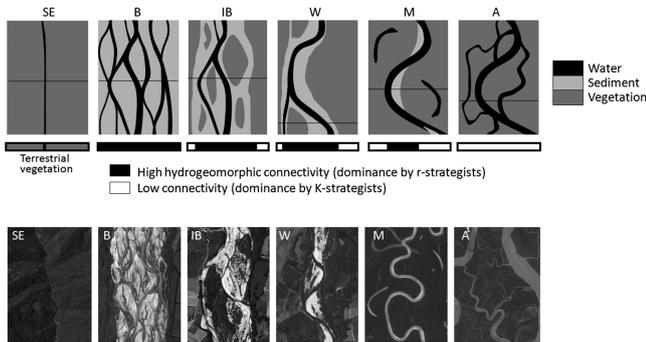


Figure 8. Transverse repartition of the two biogeomorphic process domains with: (i) high hydrogeomorphic connectivity dominated by r-strategists (resilient ecosystem); (ii) low connectivity dominated by K-strategists (resistant ecosystem). The different fluvial/biogeomorphic types are illustrated with satellite photographs taken from Google Earth™; SE: Salat River (France), 42°49′11″N, 1°11′30″E, 860 m a.s.l.; B: Rakaia River (New Zealand), 43°52′26″S, 172°11′46″E, 15 m a.s.l.; IB: Buëch River (France), 44°15′18″N, 5°51′11″E, 550 m a.s.l.; W: Orco River (Italy), 45°12′12″N, 7°50′50″E, 190 m a.s.l.; M: Juruá River (Brazil), 6°29′03″S, 68°31′47″O; A: Ganges delta (India), 22°01′46″N, 89°00′50″E, 5 m a.s.l.

the floodplain (Figures 7 and 8; Table II). Long-range inhibition takes place on the opposite bank, which is regularly eroded, leading to meander cutoff and the formation of oxbow lakes. Anastomosing rivers are dominated by a slight activation on river margins where fine sediment tends to be deposited during floods (Figures 7 and 8; Table II). Because the stream power is low in such lowland river sections, long-range inhibition is weak or inoperative.

The scale-dependent feedback enhances diversification of habitat and ecological strategies along the longitudinal dimension of the riparian ecosystem

Many palaeontological studies have shown that the modification of the fluvial environment, driven by vegetation dynamics from the Late Silurian to the Carboniferous (Davies and Gibling, 2010, 2013), was accompanied by an intense diversification of plant and faunal ecological strategies and assemblages in fluvial corridors (Beerbower, 1985; Buatois *et al.*, 1998; Labandeira, 1998; Driese *et al.*, 2000; Benton, 2010; papers in Vecoli *et al.*, 2010). This would have resulted in the potential for active construction of several new habitats, permitting the organization of contrasted ecological strategies within rivers (Bornette *et al.*, 2008; Tabacchi *et al.*, 2009).

Scale-dependent feedbacks between vegetation growth and hydrogeomorphic processes in modern rivers lead to the development of a patchy fluvial landscape along the longitudinal energy gradient. This landscape encompasses different kinds of strictly physical landforms, such as alluvial bars, and biologically engineered landforms, such as stabilized or migrating narrowed channels, accreting vegetated point bars, fluvial islands, benches, floodplain levees and oxbow lakes (Corenblit *et al.*, 2007). Such varied habitats support characteristic plant and faunal assemblages in different areas of the fluvial corridor, different seasons or succession stages and support high levels of diversity (Amoros *et al.*, 1987b; Pautou and Arens, 1994; Tabacchi *et al.*, 2009).

During the cycle of biogeomorphic succession, landform construction and related modifications of the gradient of hydrogeomorphic connectivity and habitat conditions provide new opportunities, for example for shade-tolerant riparian competitive plant species to become established within the fluvial corridor after destructive floods (Johnson *et al.*, 1976; Naiman *et al.*, 2005). Vegetation community shifts on the

upstream–downstream longitudinal gradient of rivers from the dominance of r-strategists (opportunists) to K-strategists (competitors *sensu* Grime, 2001) (Bornette *et al.*, 2008; Tabacchi *et al.*, 2009). High energy mineral fluvial types are dominated by small short-lived r-strategists that will only affect topography sporadically at a micro-scale (Figures 7 and 8; Table II). Island-braided and wandering biogeomorphic types encompass a mixture of r- and K-strategists within a shifting mosaic with a high turnover (Figures 7 and 8; Table II). Low energy anastomosing biogeomorphic type with a low turnover is dominated by tall long-lived K-strategists (Figures 7 and 8; Table II).

The duration and spatial extent of these opportunities generally increase downstream along the gradient of energy. We stress that, because the physical and chemical environment is adequately modified by plants during the FBS cycle, many aquatic and terrestrial plants and micro- to macro-faunal elements coexist currently within fluvial corridors, or start to become established on a temporary or more durable basis in intermediate to high energy reaches (Roxburgh *et al.*, 2004). For example, channel avulsions provoked by vegetation and large woody debris increase topographic heterogeneity and the formation of secondary, abandoned channels and oxbow lakes. Many aquatic and semi-aquatic plants, fauna and micro-organisms find refuge during stressful periods within these geomorphic units (Tabacchi *et al.*, 2009; Stella *et al.*, 2011).

The scale-dependent feedback enhances a transverse and vertical niche partitioning of the riparian ecosystem

As observed by Stallins and Parker (2003) in the context of barrier-island dune systems, plant-engineered geomorphic transverse and vertical gradients are partitioned into a set of spatially organized biogeomorphic domains with characteristic interactions between allogenic (hydrogeomorphic) and autogenic (biological) processes. Based on observations in different disturbed biogeomorphic systems under the control of engineer plant traits – respectively vegetated sand dune and riparian systems – Stallins (2006) and Corenblit *et al.* (2007) reached similar conclusions about how species strategies and plant assemblages operate locally along geomorphologically bio-constructed gradients. Previous ecological models had suggested passive adaptations to stress and physical disturbance as the sole operational mechanism, but these authors proposed active construction of new habitats disposed along the biologically modulated longitudinal, transverse and vertical gradients. We stress that the current hydrogeomorphic gradients and related ecological strategies (Bornette *et al.*, 2008) (Figure 9(a)) observed along temperate fluvial corridors are modulated in the long term through a complex relationship between engineer populations, community assemblage, landform-mediated disturbance gradient, and hydrogeomorphic disturbance regime. This assessment contrasts with a modulation based on the one-way respective causal importance of these factors, as proposed in earlier models of river continuum (Vannote *et al.*, 1980) and flood pulse (Junk *et al.*, 1989).

This effective niche partitioning of the riparian ecosystem by engineer plants takes place through time as a fluvial biogeomorphic succession in which the *geomorphic phase* is a rejuvenation phase of the FBS. The FBS *pioneer* and *biogeomorphic phases* are resilient transient states toward the *ecological phase* which is a resistant attractor domain (Figure 9 (b)). At initial stages of the FBS, pioneer herbaceous and shrubby plants, establishing on alluvial bars, enhance the deposition of mineral and organic matter and thus landform construction in the highly connected biogeomorphic domains of the various biogeomorphic types (Corenblit *et al.*, 2009a, 2009b) (Figure 1). Along the longitudinal energy gradient ('disturbance frequency' in Figure 9), vegetation that traps

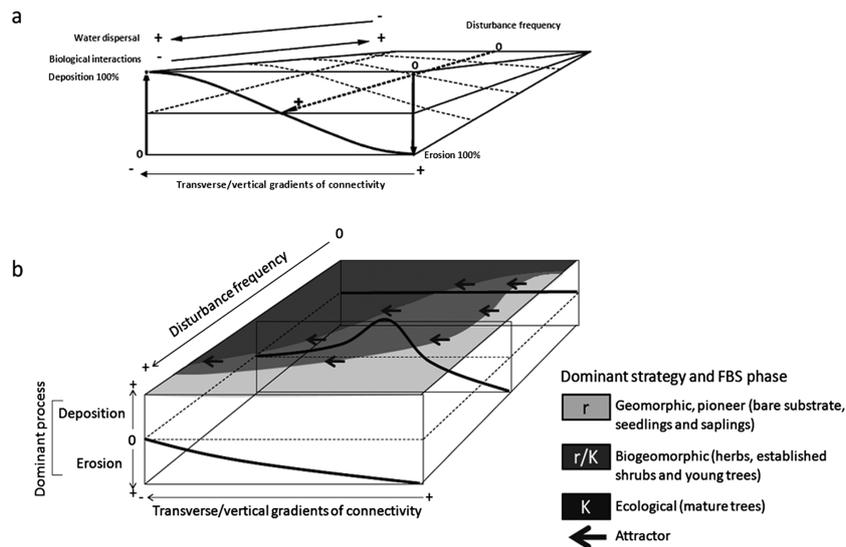


Figure 9. (a) Static model of ecological processes controlling plant communities and related strategies. Modified from Figure 3 of Bornette *et al.* (2008); (b) formulation of the previous model into a dynamic model of biogeomorphic processes controlling plant communities and related strategies. In this version vegetation is considered as an active adaptive component contributing to the construction of transverse/vertical gradients along the longitudinal dimension.

sediment and stabilizes fluvial landforms actively contributes to the modulation of the repartition of resistance and resilience strategies along the transverse and vertical dimensions (Figure 1). Channel stabilization and the growth of islands and floodplains in river sections where the strength of abiotic–biotic feedback is strong enhance the formation of a well structured transverse gradient of hydrogeomorphic connectivity, leading to distinctive biogeomorphic domains adjacent to each other and separated by ecotones (*sensu* Naiman and Décamps, 1990) (Figure 1). These biogeomorphic domains are different from the four fluvial biogeomorphic types defined above (see Table II).

The definition of biogeomorphic domains, which are necessarily characterized by the presence of vegetation, are based on submersion duration and frequency along the transverse gradient (Bornette *et al.*, 2008; Tabacchi *et al.*, 2009) (Figure 1), whereas the biogeomorphic types are defined along the longitudinal gradient. Two main biogeomorphic domains are identified: (i) the unstable disturbed riparian environment highly exposed to hydrogeomorphic disturbances and where the ecosystem is highly resilient (dominated by *r*-strategists); and (ii) the stabilized and partly disconnected riparian environment engineered by vegetation with increased resources, pedogenesis and where the ecosystem is more resistant (dominated by *K*-strategists). Corenblit *et al.* (2009a, 2009b) showed that such transverse niche partitioning is related to sediment trapping by engineer plants on the River Tech and that the spatial ratio between the two domains within the fluvial corridor depends on the balance between the hydrogeomorphic disturbance regime and the plasticity of engineer plant resistance and resilience traits (see also Corenblit *et al.*, 2010). At the community level, the authors showed a significant variation in the floristic structure between the two process domains with: (i) a very strong diversity in the highly resilient and disturbed domain dominated by *r*-strategists; and (ii) a decreased diversity in the resistant constructed domain dominated by *K*-strategists. However, Ward and Tockner (2001) noted that, as an ecological consequence, the spatiotemporal juxtaposition of habitats with contrasted conditions and strategies greatly contributes to increased gamma diversity within fluvial corridors. This increase is evident both along the longitudinal energy gradient and along the transverse gradient of connectivity at intermediate levels of disturbance, as suggested in Connell's (1978) intermediate disturbance hypothesis (Roxburgh *et al.*, 2004).

The unstable disturbed domain is subjected in high-energy reaches to frequent sediment scouring and bedload transport while fine sediment and organic matter tend to be deposited within pioneer vegetation patches leading to the emergence of the stabilized and partly disconnected domain. Consequently, biochemical and biogeochemical processes also vary drastically within these two domains (Naiman and Décamps, 1990). Anaerobic processes such as denitrification are generally effective within the vegetated domain during the biogeomorphic and ecological phases (Pinay *et al.*, 2000). Nitrate removal from interstitial waters is efficient and rapid within the plant-engineered environment (for a review see Fisher *et al.*, 2007). The engineered domain thus may be considered at the scale of the fluvial corridor as a bioconstructed nitrogen sink.

This position suggests that biogeomorphic alternative types largely differ in their functional attributes. In particular, sediment and nutrient retention in pioneer vegetated patches may promote above- and below-ground production in association with a larger nutrient pool (Fisher *et al.*, 2007). Consequently, this production may feed back on the geomorphic structure by further enhancing fine sediment retention (i.e. short-range activation) and topographic changes (Bendix and Hupp, 2000). In accordance with the functional view of Fisher *et al.* (2007), we suggest that an emerging priority is to develop a general understanding of flowpath biochemistry that encompasses the diversity of fluvial biogeomorphic types and the biogeomorphic domains, in which dissolved matter is transported by water and taken up, stored and transformed by organisms (bacteria, fungi, plants and animals).

Eco-evolutionary model: four characteristic phases of biogeomorphic organization on an evolutionary timescale

This review suggests that the path-dependent history of reciprocal interactions and adjustments between the evolution of riparian vegetation and fluvial geomorphology needs to be brought into an eco-evolutionary perspective (*sensu* Erwin, 2008; Post and Palkovacs, 2009; Matthews *et al.*, 2014). As pointed out by Gibling and Davies (2012), a hierarchy of feedbacks between riparian vegetation and fluvial geomorphology

occurred along the three spatial gradients, mainly from the mid-Silurian to the latest Carboniferous (c. 430–299 Ma), which represents the period in Earth history when the development of non-marine biogeomorphic ecosystems began to reach its culmination (see also Davies and Gibling, 2013).

The four eco-evolutionary phases

By considering the degree to which the FBS model could be applied at different intervals of the evolutionary history of terrestrialization linked to land plants, Davies and Gibling (2013) suggested that, before the colonization of continents by land plants in the Ordovician, river systems were permanently in the *geomorphic phase* of the FBS because no pioneer vegetation could colonize a river after flood (Figure 10). As such, fluvial landforms only adjusted according to geological, geomorphic and hydrological controls.

According to Davies and Gibling (2013), the *pioneer phase* of the FBS theoretically could be attainable only after the appearance of the first riparian embryophytes (Figure 10). This phase became possible due to the first abundant generations of small, primitive, rooted pioneer land plants, capable of responding to immersed conditions and to an unstable and fluctuating fluvial environment. The *biogeomorphic phase* of the FBS was probably not achieved until after the late Silurian to earliest Devonian (Figure 10). This phase was characterized by strong eco-evolutionary feedbacks between vegetation evolution and hydrogeomorphology with the appearance of new biogeomorphic types and a second generation of biotic responses (e.g. the evolution of deeper roots, higher size and seeds) related to a constructing and stabilizing riparian environment. Davies and Gibling (2013) suggested that the *ecological phase* of the FBS could only be reached from the Carboniferous onwards, once competitive plant traits, related to colonizing an aggraded and stabilized riparian environment, had evolved (Figure 10).

This chronosequence thus encompasses three fundamental steps: (i) the evolution of functional response traits of engineer plants which increased their resistance and resilience within a terrestrial physically disturbed environment (pioneer phase); (ii) the effects of established engineer plants on their

geomorphic environment (biogeomorphic phase); and (iii) the evolution of functional response traits of both engineer and other accompanying taxon to the environmental modifications under biotic control (ecological phase). We suggest that the model of niche construction proposed by Odling-Smee *et al.* (2003) may be compatible with this eco-evolutionary chronosequence.

Is the FBS compatible with the concept of niche construction? Wright (2009) and Wright *et al.* (2012) stressed that engineer species almost certainly change selection pressures in largely modified environments through niche construction (NC) (*sensu* Laland *et al.*, 1999; Odling-Smee *et al.*, 2003). NC refers to the case when the evolutionary dynamics of the engineer species or others species within the ecosystem are modified through changes in one or more dimensions of the physical environment (Matthews *et al.*, 2014). By definition, NC operates with an evolutionary response within the ecosystem engineered by living organisms. Alluvial landforms durably engineered by organisms were considered by Steiger and Corenblit (2012) in the scope of the NC framework as the signature of feedback between hydrogeomorphic processes and plant evolution, supporting the emergence of what they have called ‘evolutionary geomorphology’.

As highlighted above, the long-term effects of riparian niche-constructing plant species on fluvial environments are, at the scale of the fluvial corridor, large and durable. Throughout Earth history, the first appearance of engineer plants, and thus the persistence or systematic recurrence of specific kinds of modified (biologically constructed) riparian habitats and gradients, would have been a major selective force for plant functional traits and ecological strategies within partitioned riparian ecosystems (Fisher *et al.*, 2007; Gibling and Davies, 2012; Davies and Gibling, 2013). Hydrogeomorphic parameters (e.g. topography, sediment texture, hydrogeomorphic connectivity) adjusted as the engineer-traits of plants evolved, particularly from the end of the Silurian onwards. In turn, this adjustment continually influenced plant evolution and riparian ecosystem structure and function, ultimately leading to the emergence of riparian biogeomorphic ecosystems (Figure 10).

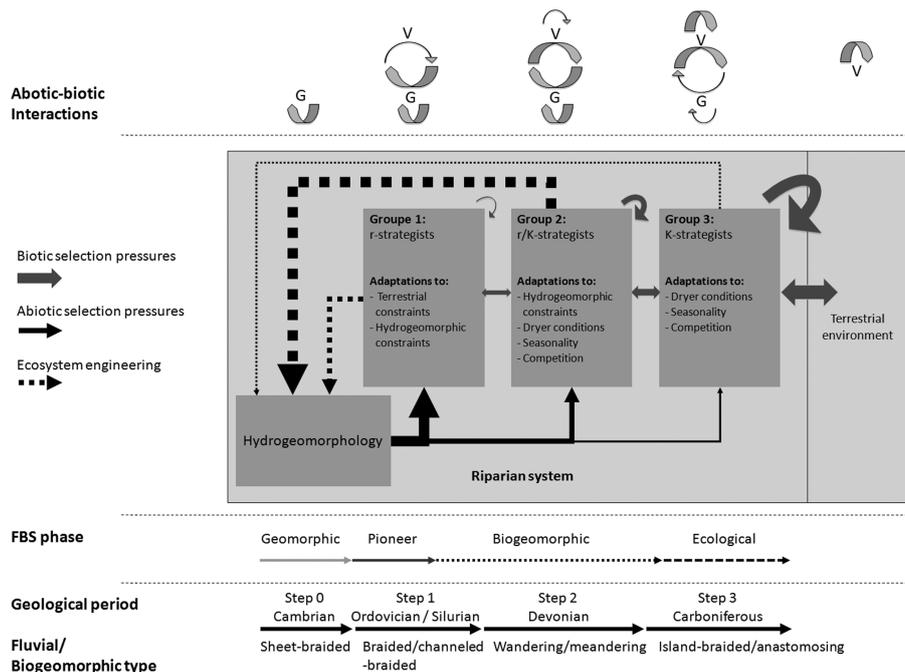


Figure 10. Biogeomorphic eco-evolutionary model of reciprocal interactions and adjustments between vegetation evolution and fluvial dynamics on geological time-scales. V = vegetation; and G = geomorphology.

These successive generations of biotic selections and related geomorphic changes finally resulted in the emergence of the main fluvial biogeomorphic types (FBT) observed today (Table II). We suggest that contemporary fluvial hydrosystem gradients and associated community structure and function emerged from these long-term feedback dynamics between vegetation evolution and river dynamics (Fisher *et al.*, 2007; Corenblit *et al.*, 2009b). The related gradients of ecological strategies observed along spatial and temporal river dimensions probably arose from evolutionary trade-offs and cost–benefit among plant species in an environment in which stabilized and disconnected domains developed progressively at the margins of disturbed and unstable domains. The concepts of NC and ecological inheritance (*sensu* Odling-Smee *et al.*, 2003) appear to be potentially useful in describing such dynamics (Gibling and Davies, 2012; Corenblit *et al.*, 2014). Niche-constructed habitats and gradients may lead to very important and recurrent modifications in species interactions and community traits within the riparian system at ecological timescales (Corenblit *et al.*, 2009a, 2009b). Francis *et al.* (2009) and Corenblit *et al.* (2009b, 2014) suggested that certain fluvial landforms engineered by pioneer riparian species, such as fluvial islands and benches, improve the fitness of the engineer species themselves, as well as other species within the ecosystem. Rood *et al.* (2011) recently demonstrated that fine-sediment deposition favours willow establishment and clonal expansion, and that the canopies protect and trap sand in a feedback that sustains surface sand and sand-bar willows. Such landforms are beginning to be considered as positive niche constructions, and thus as functional ecological components of the fluvial hydrosystem (Fisher *et al.*, 2007; Corenblit *et al.*, 2010, 2011, 2014).

Concluding Remarks

This review paper suggests that a fuller comprehension of riparian ecosystem structure and stability depends on our ability to conceptualize and analyze both ecological (contemporary) and evolutionary (ancient) abiotic–biotic feedbacks. Such feedbacks operate between small-scale biological phenomena (genotypic selection and phenotypic expression of biological traits at the organism/population level) and patch-scale ecological and hydrogeomorphic processes (fluvial landform and plant community adjustment).

A huge conceptual, methodological and technical research effort still remains to be carried out at the interface between several disciplines to integrate the evolutionary dimension of rivers within a four-dimensional framework. One difficulty will be to identify and to interlink the ecosystem integration levels affected by engineer activities. Dawkins (2004) and Matthews *et al.* (2011) pointed out that evolutionary responses of populations to engineer activities within an ecosystem may be varied. The engineer species itself may be concerned exclusively, with the selection of new anatomical, physiological or life-history traits related to its niche construction, or even the selection of engineer-alleles that improve the ability to construct niches (extended phenotype *sensu* Dawkins, 2004). Evolutionary responses may in other cases concern only other species present in the ecosystem; they may even provide a feedback to the engineer species through the selection of alternative traits for other species that influence the engineer species, for example through predation, competition, or symbiosis. These examples are only some among many theoretical possibilities of combinations of eco-evolutionary interactions within the riparian system.

We suggest that forging a functional classification or hierarchy of eco-evolutionary interactions within the riparian context

represents a fundamental challenge and step toward the integration of abiotic–biotic feedbacks within the four-dimensional framework of river dynamics. Concepts set out in the niche construction framework will also have to be formulated as operational working hypotheses to be tested in ways suggested by Corenblit *et al.* (2014) and Matthews *et al.* (2014).

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