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Interactions between vegetation and river morphodynamics. Part I: Research clarifications and challenges

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ABSTRACT

Rivers have an intricate relationship with the vegetation that colonizes them. Riparian plants, capable of thriving within river corridors, both respond to and influence geomorphology. Yet interactions between river morphodynamics and vegetation tend to be context specific, making it challenging to generalize findings between locations. The current comprehension of vegetation interaction with physical processes, and especially its effects on river morphodynamics, still lacks clarity. This article examines numerous sources of variation in plant responses to, and effects on, river morphodynamics. Vegetation influences on geomorphological parameters vary in terms of intensity and spatial extent along the gradient of river energy and according to the fluvial style. Whilst feedbacks between vegetation and river morphodynamics are readily discernible at a local scale, on larger spatial scales, it can remain difficult to precisely determine cause-and-effect relationships that link hydrogeomorphic and vegetation drivers and the outcomes of their feedbacks. This is especially problematic for those feedbacks that give rise to emergent system landscape behaviour in meandering and island braided rivers. By contrast, in certain river configurations, such as anabranching rivers, the imprint of vegetation on the riverscape can be clearly evident. The imprint of vegetation is also supported by evidence from the ancient alluvial record. Through this review, we highlight key perspectives from a wide range of modern and ancient rivers of varied configuration in order to inform future studies of vegetation responses to, and effects on, river morphodynamics.

1. Introduction

Rivers are among the most dynamic landscapes on Earth, constantly adjusting their geomorphology according to water and sediment flows (Leopold and Maddock, 1953; Leopold and Wolman, 1957; Ward et al., 2001; Ahmed et al., 2019). They are major aquatic-terrestrial interfaces

that are characterized by strong longitudinal (up-valley/down-valley) and transversal (cross-valley) physicochemical gradients related to shear stress, soil moisture, flooding frequency, sediment texture and cohesion, organic matter, and nutrient content (Naiman and Décamps, 1997; Pautou et al., 1997; Ward, 1998; Steiger et al., 2005). Rivers also hold an entangled association with the vegetation that colonizes them; a

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relationship with an extensive deep time history. After the first land plants evolved from freshwater charophyte algae in the Early Ordovician Period (ca. 480 Ma) (Strother and Foster, 2021), river channels and their floodplains have been a prime theatre for evolutionary innovation in plant lineages and feedbacks throughout geological history (Davies and Gibling, 2011; Corenblit et al., 2014; Ielpi et al., 2014; Buatois et al., 2022).

The strong ecological gradients present in rivers have exerted selection pressures on plant establishment and their characteristics, which work as filters governing plant assemblages in various biomes across longitudinal, transversal and vertical dimensions, and across a multitude of timescales (Greb et al., 2006; Falcon-Lang et al., 2011; Fielding et al., 2011; Gibling and Davies, 2012; Stein et al., 2012). As ancient land plants developed in stature and habitat utilization, from small vascular plants restricted to coastal lowlands to tall trees with deep roots on floodplains and adjacent environments, they simultaneously revolutionized hydrogeomorphological processes and channel-floodplain adjustments (hereafter 'river morphodynamics'). The earliest plants bounded fine-grained sediment, capturing this material within river systems for the first time (McMahon and Davies, 2018a; Mitchell et al., 2023) and, later, more arborescent plants enhanced bank stabilization and floodplain construction, encouraging both meandering and anastomosing fluvial planforms. These changes in fluvial style occurred in environmental settings where there would otherwise be a surplus of sediment and uncorralled channels, prohibiting their formation (Corenblit et al., 2009a; Davies and Gibling, 2011; Ielpi et al., 2014).

In extant rivers, pioneer conceptual models helped to describe and understand how vegetation responds to hydrological and geomorphological conditions, mainly as a function of gradients of exposure to floods and resources (for a review, see Tabacchi et al., 1998; Tabacchi and Planty-Tabacchi, 2001; Steiger et al., 2005; Bornette et al., 2008). At the individual and population levels, specific plant morphological, biomechanical, physiological, phenological and life history characteristics have been interpreted as adaptations to the physicochemical conditions, e.g., hydrological variability, prolonged submersion, shear stress, sediment erosion and burial, drought and nutrient availability (Junk et al., 1989; Naiman and Décamps, 1997; Shafroth et al., 1998; Edwards et al., 1999; Rood et al., 2000; Karrenberg et al., 2002; Lytle and Poff, 2004; Stella et al., 2006; Bornette et al., 2008). At the community level, vegetation assemblages have been related to the filtering of plant strategies and niche partitioning along the spatiotemporal gradients (Townsend and Hildrew, 1994; Tabacchi et al., 2000; Steiger et al., 2005; Bornette et al., 2008; Harezlak et al., 2020). Bornette et al. (2008) proposed a model of plant strategies in temperate rivers that incorporates hydraulic and geomorphological features that govern plant recruitment, establishment, and growth along a transversal gradient from the main channel to the floodplain. The model elucidates how the disturbance gradient and bedload grain size influence the relative balance between erosional and depositional processes, and how the frequency of flood disturbance modulates the intensity of these processes and ultimately controls the spatiotemporal distribution of plant species strategies and assemblages.

Riparian plants can act as geomorphological agents within river corridors both when they are alive, by protecting sediment from erosion with roots, rhizomes and flattened aerial parts, and trapping sediment and organic matter with above-ground structures (Gurnell, 2014), and when they are dead, by providing a supply of wood pieces that may act individually or coalesce as jams (Gurnell et al., 2002). Models have conceptualized the effects of vegetation on river morphodynamics from an ecological perspective (for details, see Part II; Gurnell and Gregory, 1995; Tabacchi and Planty-Tabacchi, 2001; Gurnell and Petts, 2006; Osterkamp and Hupp, 2010). Several studies and models have also considered the physical effects of vegetation on hydraulics (Petryk and Bosmajian, 1975; Nepf, 1999; Nepf and Vivoni, 2000; Järvelä, 2002; Green, 2005; Zhao et al., 2016), on sediment transport (Li and Shen, 1973; Elliott, 2000; Righetti and Armanini, 2002; Samani and Kouwen,

2002; Rominger et al., 2010; Meire et al., 2014; Manners et al., 2015) and on river morphodynamics (Gibling et al., 1998; Rowntree and Dollar, 1999; Gurnell et al., 2001; Bennett et al., 2002; Tooth and Nanson, 2004; Tooth and McCarthy, 2004; Tooth et al., 2008; Corenblit et al., 2009a; Gurnell, 2014; Manners et al., 2014; Corenblit, 2018). For example, Bennett et al. (2002) conducted a flume experiment that showed that river channel expansion and widening, thalweg meandering, and the development of riffles and pools are affected by discrete plantings of rigid emergent structures imitating vegetation, and that the extent of channel changes is influenced by the shape of the vegetation zone and the density of the vegetation.

Biogeomorphological investigations of the role of vegetation in modulating river morphodynamics tend to focus on humid temperate, semi-arid and sub-humid climatic contexts, and on braided, meandering, anastomosing and anabranching fluvial styles. Empirical evidence arises mainly from detailed disciplinary case studies at specific study sites and specific spatiotemporal scales (Graf, 1978; Rodrigues et al., 2007; Corenblit et al., 2009b; Gurnell et al., 2001, 2013; Wintenberger et al., 2015; Gurnell and Grabowski, 2016). Any generalization of these results/effects, especially those occurring at a local site, remains challenging.

The lack of clarity in our current understanding of the interaction of vegetation and river morphodynamics arises because vegetation effects are not easy to isolate and measure in the field. The first major challenge is the relative absence of rivers on Earth where vegetation has never historically acted (i.e. was never present at any stage), even in the most arid regions (Drake et al., 2011), prohibiting clear isolation of its effects from other physical drivers in field studies. A second challenge is that interactions between vegetation and river morphodynamics are highly sensitive to modulation by species effects, species assemblages, environmental conditions, and spatiotemporal context (Steiger et al., 2005; Gurnell, 2014; Diehl et al., 2017), negating the possibility that any one field site will yield universally applicable information on these interactions. A third challenge is that vegetation is only ever just one component of a larger system of interdependent biotic and abiotic controls on river dynamics. The importance of vegetation as a geomorphological agent and its connectivity to other parts of the system change even within one specific field site, depending on the time and place it is being studied and the evolutionary legacy of plant-water-sediment interactions that are now imprinted in the current system. Together, these challenges have historically hindered the conceptualization, isolation and quantification of vegetation effects on river morphodynamics.

In this review, we provide clarifications and present new conceptual and methodological frameworks needed to improve our capacity to isolate and understand vegetation effects on river morphodynamics. The review assesses the challenge of disentangling the effects of vegetation on river morphodynamics and discusses key research challenges. Amongst these are the isolation and quantification of plant effects using mechanical and statistical approaches, the upscaling of generalizations from the micro-habitat scale to the corridor scale, the utilization of new technologies with enhanced temporal and spatial frequency and resolution, the assessment of how global environmental change could influence the relationships between riparian vegetation and river morphodynamics, and the improvement of the understanding of ancient rivers operating at different stages of plant evolution.

2. Vegetation responses to, and effects on, river morphodynamics are interrelated

It is now widely accepted that vegetation affects river morphodynamics and habitat properties in different biomes, in different hydrological, geomorphological, and anthropogenic contexts, and across various spatiotemporal scales (see Gurnell and Gregory, 1995; Tabacchi et al., 2000; Steiger et al., 2005; Corenblit et al., 2007; Gurnell et al., 2012; Albertoni et al., 2014; Gurnell, 2014). The effects of vegetation have been studied using different investigative approaches: (i) empirical

observations in the field (Fielding and Alexander, 1996; Rowntree and Dollar, 1999; Gurnell et al., 2001; Rodrigues et al., 2006, 2007; Corenblit et al., 2009b; Bertoldi et al., 2011a; Török and Parker, 2022); (ii) spatial analyses using remote sensing imagery (Hickin and Nanson, 1984; McKenney et al., 1995; Friedman and Lee, 2002; Brooks et al., 2003; Corenblit et al., 2010; Piégay et al., 2020); (iii) *ex situ* flume experiments (Tsujiimoto, 1999; Nepf and Vivoni, 2000; Bennett et al., 2002; Järvelä, 2002; Tal et al., 2004; Hooke et al., 2005; Luhar et al., 2008; Tal and Paola, 2010; Zong and Nepf, 2010; Folkard, 2011; Siniscalchi et al., 2012; Bertoldi et al., 2015; Yang et al., 2018); and (iv) numerical modelling of river morphodynamics, sometimes coupled with ecological (vegetation) models with different degrees of complexity (Darby, 1999; Green, 2005; Perucca et al., 2006; Jang and Shimizu, 2007; Perucca et al., 2007; Perona et al., 2009; Crosato and Saleh, 2011; Camporeale et al., 2013; Coulthard et al., 2013; García-Arias et al., 2013; Bertoldi et al., 2014; van Oorschot et al., 2016; Martínez-Fernández et al., 2018).

In riparian habitats, plant morphological properties (e.g., plant size, frontal area with or without leaves, root architecture), biomechanical characteristics (e.g., flexibility, resistance to breakage and uprooting) and spatial distribution (e.g., density and spacing) have been shown to

influence water flow properties, sediment transport and trapping, soil development and fertility, and landform stabilization (Fig. 1) (Bennett et al., 2002; Lightbody and Nepf, 2006; James et al., 2008; Mineau et al., 2011; Mineau et al., 2012; Luhar and Nepf, 2013; Meier et al., 2013; Perignon et al., 2013; Bätz et al., 2015; Manners et al., 2015; Politti et al., 2018; Licci et al., 2022; Mitchell et al., 2023; O'Briain et al., 2023). In aquatic habitats, similar attributes have been identified, whereby macrophytes enhance the deposition and stabilization of fine sediment, with consequent feedback on plant growth (Gurnell et al., 2006; Jones et al., 2012; Albertoni et al., 2014). The nature of the feedback depends on the rate of sediment deposition and the physico-chemical properties (sediment texture, organic matter, pH, N, P, K, Mg, Ca and S content) of the material that plants trap. Changes in plant community can occur when the deposited sediment is finer and more nutrient rich than it was at the initial stage of plant development (Jones et al., 2012).

Despite recognizing vegetation as a major component influencing river morphodynamics (e.g., Corenblit et al., 2007; Gurnell, 2014), specific vegetation effects on river morphodynamics still need to be clearly distinguished from exclusively hydrogeomorphological factors controlling fluvial trajectories of change. Our ability to properly isolate

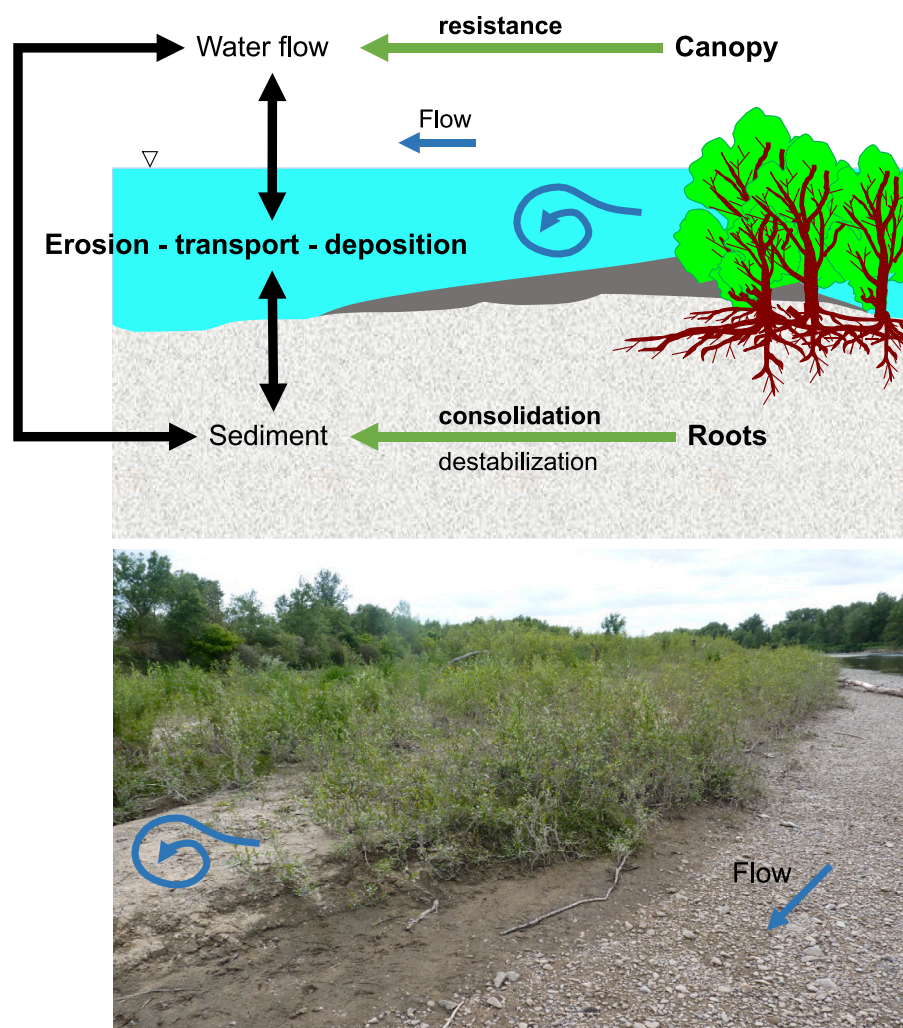


Fig. 1. Simplified model of local vegetation effects on water flow and sediment dynamics. The model considers the effects of the roots on sediment stability and the effects of the submerged canopy on flow properties and sediment transport. The green arrows illustrate the effect of above- and below-ground vegetal structures on water flow properties and on sediment trapping and cohesion. The blue circular arrows illustrate a significant decrease in velocity, while the linear blue arrows indicate an increase in velocity. Destabilization of sediment by the plants occurs when the threshold of uprooting is exceeded. The black arrows establish the linkages between hydraulic and sediment dynamics. The photograph illustrating the effect of vegetation on sediment trapping was taken on the Allier River, France. Photograph: B. Hortobágyi. Adapted from Corenblit et al. (2007).

and describe plant effects on river morphodynamics remains incomplete and sometimes results in biases or misinterpretations.

In the last thirty years, there has been a growing effort to examine the interactions between vegetation and river morphodynamics across various types of rivers and bioclimatic regions. All these studies have contributed to the acknowledgement that the responses of riparian vegetation to, and its effects on, river morphodynamics involve a vast array of situations influenced by local to regional climatic, fluvial (hydrogeomorphological), anthropogenic and biological modulators (Tables 1-4).

Landform responses to external environmental stimuli are often complex and non-linear (Phillips, 2006). In the case of vegetated rivers, a major issue originates from the fact that plants and physical components of rivers are embedded in a 'complex adaptive system' *sensu* Levin (1998). A complex adaptive system is a system in which Darwinian selection processes at the lower levels of biological organization (genes, individual organisms, and populations) potentially lead to the emergence and self-organization of higher-level ecosystems as described by Erwin (2008), including landform and landscape components (Corenblit et al., 2011). In such a system, ecological, evolutionary and physical processes are explicitly considered to affect each other in feedback loops over geological/evolutionary timescales (Fig. 2).

All associations between fluvial landforms and vegetation are to be considered as potential signatures of unidirectional or bidirectional functional linkages between plants and river morphodynamics. Functional linkages here refer to: (i) how geomorphology modulates vegetation spatial distribution, life history, and morphological and biomechanical characteristics; (ii) how vegetation modulates geomorphology; and (iii) how abiotic-biotic feedbacks can lead, in certain cases, to the occurrence of characteristic biogeomorphological units (e. g., vegetated ridges, fluvial islands and floodplains) that ensure the survival, growth and reproduction of the engineer plants and/or other plant species during the succession (Fig. 3) (Corenblit et al., 2015). The three components of biogeomorphological functionality described above can occur independently or in combination, depending on the environmental and biological contexts.

A challenge is to unequivocally and formally establish the distinction between the following cases: (i) where abiotic-biotic feedbacks become dominant in shaping river morphodynamics (Fig. 3a); (ii) where vegetation predominantly responds to river morphodynamics without significantly affecting it (Fig. 3b); and (iii) where vegetation predominantly affects river morphodynamics (Fig. 3c).

3. Plants drive scale-dependent feedbacks at local scales with potential effects at larger scales

A difficulty in establishing the linkages between vegetation and river morphodynamics arises from the fact that interactions between geomorphology, vegetation and resulting spatial patterns are highly variable in both space and time in terms of their quality, intensity and frequency (González del Tánago et al., 2021). Plant effects occurring at local scales (10^1 - 10^2 m), with one to several aggregated individuals affecting sediment dynamics, are generally conceptually and physically easier to delineate. For example, Nakayama et al. (2002) documented the formation of obstacle marks caused by vegetation in a sub-humid context in the Burdekin River, Queensland, Australia. These obstacle marks comprised well-defined erosional scour and depositional sediment tails downstream of vegetation obstacles. The resulting local geomorphology, composed of a characteristic arrangement of aggradation and degradation zones, clearly demarcates from its initial abiotic geomorphological matrix. Such patterns have been successfully described in the temperate biome using the framework of 'scale-dependent feedback' (Gurnell et al., 2005; Francis et al., 2009; Corenblit et al., 2015; Larsen, 2019; Cornacchia et al., 2020; Licci et al., 2022). Scale-dependent feedback occurs within the riparian context where, at the local scale, plant individuals or communities enhance sediment

Table 1

Climatic modulators of vegetation responses to, and effects on, river morphodynamics.

Modulator	Vegetation responses to, and effects on, river morphodynamics	References
Climatic context	Climate modulates the responses to, and effects of, vegetation on river morphodynamics by controlling temperature, precipitation and incident radiation. These are factors that affect vegetation recruitment, establishment, phenology, growth, composition and succession within fluvial corridors.	Dodds et al. (2015).
Cold (polar)	Vegetation development is impeded.	Larone and Reid (1993); Walker and Hudson (2003).
Cold (tundra)	River channels adjust in response to physical interactions between water, sediment, ice flows and frozen banks. Vegetation is limited to dwarf shrubs, sedges and grasses, mosses, and lichens.	Gyssels et al. (2005); De Baets et al. (2006); Matsubara et al. (2015); Chassiot et al. (2020).
Cold (taiga)	Only the smallest channels of a few meters in width and a few decimeters in depth are affected by herbaceous and dwarf shrub roots. These vegetation types stabilize banks and lead to the formation of stable meanders or anastomosing channels in small lowland rivers. The morphodynamics of periglacial, larger, deeper rivers with taller banks remain controlled by physical processes. Boreal forests.	Nanson and Beach (1977); Huisink et al. (2002).
Arid	Riparian forests can affect the morphodynamics of large rivers, favouring confined braided and island braided patterns in piedmont areas, and wandering and meandering patterns in lowlands. The dense forest cover is a key factor for the meandering morphology, as it decreases coarse sediment supply from the catchment and prevents braided conditions. Vegetation development is impeded.	Reid and Frostick (2011).
Semi-arid and sub-humid	Channels may adjust in response to aeolian-fluvial interactions and physical properties of river banks. Occurrence of vegetation in the active channel where water flow is intermittent or perennial, and when groundwater is shallower. Vegetation can form patches, elongated ridges in the channel bed, and even a dense gallery of trees at the channel margins in sub-humid conditions.	Stromberg and Patten (1990); Nanson and Knighton (1996); Gasith and Resh (1999); Tooth and Nanson (2000); Corenblit et al. (2009b, 2010); Underwood et al. (2009); Stella et al. (2013a, 2013b); Stromberg and Merritt (2016).
	During flash floods or flood season, vegetation patches or gallery forests protect river bed and banks from erosion and trap	

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Table 1 (continued)

Modulator	Vegetation responses to, and effects on, river morphodynamics	References
	fine sediment in the floodplain.	
	A diverse array of fluvial styles controlled by vegetation can be observed in semi-arid and sub-humid contexts, such as confined braided, anabranching, wandering and meandering rivers.	
Humid temperate and tropical	Occurrence of dense and vertically complex riparian forests with diverse morphotypes.	Salo et al. (1986); Junk et al. (1989); Pautou et al. (1997); Muñoz-Mas et al. (2017); Corenblit et al. (2009b); Walcker et al. (2021).
	Vegetation can influence river morphodynamics within entire fluvial corridors, including across wide floodplains, particularly in lowlands where physical energy is low and sediment is cohesive.	

trapping, increase resource availability, and decrease shear stress, thereby promoting plant survival, growth and succession through ecosystem engineering mechanisms. Conversely, these individuals and communities reduce resources and amplify shear stress over longer distances at their margin (for a detailed description, see Francis et al., 2009). Conceptual models deriving from this framework were proposed for analysing sediment tails, fluvial islands, and vegetated bar construction in rivers at local scales (Fig. 4a-c) (Gurnell et al., 2001; Gurnell and Petts, 2002, 2006; Nakayama et al., 2002; Rodrigues et al., 2006, 2007; Schoelynck et al., 2012; Corenblit et al., 2016b; Hortobágyi et al., 2018).

In particular, Gurnell et al. (2001) provided a comprehensive conceptual model of fluvial island construction in a high-energy reach of the Tagliamento River, Italy, located in the temperate biome, illustrating short-range, small-scale positive feedbacks (i.e., a self-reinforcing loop enhancing the original signal or input) of vegetation growth and succession with landform construction and stabilization. In this model, a positive feedback ('short-range activation' in Fig. 4) of matter and resource accretion (i.e., water, nutrients and organic matter) is expected in a vegetation stand or in an accumulation of dead wood that forms a stable dissipative structure in the flow, and also downstream from the stand or dead wood in the tail. Negative feedback ('long-range inhibition' in Fig. 4) of increased turbulence and erosion can then occur upstream and around the vegetation stand (Gurnell et al., 2001, 2005; Rietkerk et al., 2004; Francis et al., 2009). One advantage of such a model is the possibility to mechanically or statistically test hypotheses related to plant effects at local scales using flume or field investigative approaches, and then formally establish the covariation between plant morphological and biomechanical characteristics and local geomorphology with repeated measurements in time (van Wesenbeeck et al., 2008; Bouma et al., 2009, 2013). The resulting effects of vegetation on erosion and landform construction with varying flow velocity/height and sediment transport can then be analysed.

Other models have considered plant effects at larger scales, describing riverbank dynamics (Thorne, 1990; Abernethy and Rutherford, 1998), floodplain accretion (Pautou et al., 1997; Bendix and Hupp, 2000), and fluvial landscape dynamics such as the 'shifting mosaic steady-state' (Bormann and Likens, 1979; Stanford et al., 2005; Garófano-Gómez et al., 2017). Conceptual biogeomorphological models developed in the last decades more explicitly consider feedbacks between vegetation and river morphodynamics at the corridor scale. Corenblit et al. (2007) proposed the Fluvial Biogeomorphological Succession (FBS) model and its four phases (Fig. 5; see also Corenblit et al., 2009b, 2015; Corenblit, 2018). The geomorphological phase (G in

Table 2

Fluvial modulators of vegetation responses to, and effects on, river morphodynamics.

Modulator	Vegetation responses to, and effects on, river morphodynamics	References
River type	The ability of vegetation to establish within the fluvial corridor and modulate river morphodynamics varies according to the river type (or river style). The river type is intricately linked to the complex relationship between hydrological regime, specific stream power, sediment supply, and their spatiotemporal variations.	Gurnell et al. (2012, 2016); Gurnell (2014).
	The quantity of transported sediment and the balance between the transport of coarser bedload and finer sediment suspended load are crucial in determining the river type.	
	The effect of vegetation on alluvial river planform changes in both quality and intensity along gradients of adjustments between the hydrogeomorphological variables. Vegetation itself can play a critical role in controlling the river type.	
Straight confined and actively braided rivers	Flash floods, high shear stress and high bedload transport rates can outweigh vegetation's mechanical resistance and its capacity to establish permanently. River morphodynamics remains predominantly physically driven.	Rust (1972); Ashmore et al. (2011).
Island braided, wandering and anabranching rivers	Pioneer vegetation and in-channel wood can trap sediment locally, forming accretion points within the active channel.	Gurnell et al. (2001, 2005); Gurnell and Petts (2002, 2006); Sandercock et al. (2007); Erskine et al. (2009); Belletti et al. (2013); Wintenberger et al. (2015); Gurnell and Bertoldi (2020).
Meandering rivers	River morphodynamics can be modulated by vegetation during cycles of formation and erosion of fluvial islands, and of vegetated ridges and benches contouring the active channel. Such cycles extend over a few years to a few decades, depending on the flood regime. The effects of vegetation can span from decades to centuries. Along a free meandering reach, vegetation can trap and stabilize large quantities of fine sediments on point bars during annual to decadal floods. Accreting point bars are progressively incorporated into the floodplain as scroll bars	Nanson and Beach (1977); Salo et al. (1986); Corenblit et al. (2016a, 2016b); Zen et al. (2017); Kleinhans et al. (2019); Walcker et al. (2021).

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Table 2 (continued)

Modulator	Vegetation responses to, and effects on, river morphodynamics	References
Anastomosing rivers	(scroll ridges) as the channel migrates and as the surface of the bar rises and vegetation develops. In lowland low-energy river reaches, extensive floodplain forests can stabilize multiple channels and contribute to the trapping of silt and clay. These processes contribute to long-term floodplain and delta construction.	Hupp (2000); Volke et al. (2019).
River size	Channel width and depth, which are controlled by local geological settings and flow and sediment regimes in alluvial systems, modulate vegetation responses and effects.	Anderson et al. (2004).
Small lowland rivers	The morphodynamics of small lowland rivers, from a few meters to tens of meters wide, can be drastically affected by aquatic macrophytes, grasses, shrubs and trees that control bank stability and channel geometry. Along small rivers, banks that are heavily colonized by dense grass result in highly resistant banks and narrower channels. Conversely, woody vegetation can increase geomorphological instability in small rivers. When the size of in-channel wood pieces is larger than the channel width, they may generate obstacles and potentially increase local bank erosion and trigger channel avulsion. Vegetation colonizing alluvial surfaces on the channel bed increases flow resistance, reduces flow velocity and retains sediment, inducing channel narrowing.	Bilby and Likens (1980); Cherry and Beschta (1989); Fetherston et al. (1995); Abbe and Montgomery (1996); Huang and Nanson (1997); Piégay and Gurnell (1997); Abernethy and Rutherford (1998, 2001); Kirchner et al. (1998); Collins and Montgomery (2002); Anderson et al. (2004); Gurnell et al. (2006); Pollen-Bankhead and Simon (2010); Gurnell et al. (2012, 2016); Gurnell and Grabowski (2016).
Large rivers	Vegetation affects large river morphodynamics through the narrowing of channels when banks are colonized by trees, in contrast to banks with grass only or banks with no vegetation. The increase in bank stability induced by trees occurs where bank height does not exceed rooting depth. Vegetation roots have reduced effects on channel bank stability in larger rivers, when banks are sandy and when they are too tall to be protected by root systems. Mass failure can be exacerbated where tall and heavy trees are undermined below their rooting depth, and this undermining can lead to major bank erosion when they fall into the channel. Dead roots and root holes in riverbanks can enhance seepage	Thorne and Tovey (1981); Kondolf and Curry (1984); Thorne (1990); Abernethy and Rutherford (1998); Gaskin et al. (2003); Anderson et al. (2004); van De Wiel and Darby (2007); Samadi et al. (2013); Zhu et al. (2018); Simon and Collison (2002); Ielpi and Lapôtre (2019); Chassiot et al. (2020).

Table 2 (continued)

Modulator	Vegetation responses to, and effects on, river morphodynamics	References
	and tensile cracks, and subsequently induce mass failure, particularly along tall banks of silt and sand.	
Relative elevation	Conversely, dense vegetation cover on floodplains of large rivers can prevent cutoffs in meandering reaches and enhance planform stability and sediment trapping during high-magnitude flood events by slowing down water flow. Groundwater table level is a key driver of vegetation biomass within the active channel. Relative elevation of alluvial bars thus is crucial within active river channels, especially in semi-arid or sub-humid channels subject to permanent or prolonged summer drought and/or variable but frequent scouring.	Cooper et al. (1999, 2003); Scott et al. (2000); Meier (2008); Mouw et al. (2009); Corenblit et al. (2010); Meier and Hauer (2010); Stella et al. (2013a); Gurnell (2014); Bätz et al. (2016); Gurnell et al. (2016); Sargeant and Singer (2016).
Physicochemical properties of the sediment	The elevation at which vegetation develops is strongly influenced by water availability and flood discharge. Vegetation can colonize the same river, either from the margins of the low-flow channel or from the tops of bars, depending on the seasonal and interannual variations in low and high water levels and flood sequence. Physicochemical properties of deposited sediment affect vegetation growth and succession, and hence the potential of vegetation to affect sediment dynamics, so forming a feedback loop. Sediment texture is a critical driver of moisture retention and diffusion; e.g., pockets of moist fine sediments in the alluvium can be exploited by trees for survival during drought periods. Local fine sediment trapping, combined with organic matter and nutrient enrichment promoted by vegetation itself, control plant growth rate, above- and below-ground biomass ratio and roots architecture (e.g., deeper/larger if the soil is poor, and shallower, longer, and more ramified if the surface layer is finer and richer in nutrients). The enrichment of fine sediment, nutrients, organic matter and seeds in vegetation-initiated and constructed landforms supports the germination and growth of aquatic and riparian plants, some of which would otherwise establish in very limiting environmental conditions	Barko et al. (1991); Chambers et al. (1991); Boeger (1992); Carr (1998); Ságová-Marečková et al. (2008); Jones et al. (2012); Cornacchia et al. (2019); Licci et al. (2022).

Table 3

Anthropogenic modulators of vegetation responses to, and effects on, river morphodynamics.

Modulator	Vegetation responses to, and effects on, river morphodynamics	References
Anthropogenic impacts	The putative Anthropocene time interval is characterized by drastic alterations to the structure and function of rivers at a global scale, with most rivers worldwide being directly and indirectly impacted by human activity. Human impact alters the ways vegetation responds to, and affects, river morphodynamics.	Friedman et al. (1998); Millennium Ecosystem Assessment (2005); Gregory, 2006; Habersack et al. (2014); Wohl (2020).
Global scale impacts	Human activities impact climate, inducing changes to the water cycle and temperature regimes with pervasive indirect impacts on the degree to which vegetation may influence river morphodynamics. For example, anthropogenic climate change is causing increased polar and alpine ice melt, more frequent extreme floods and droughts in temperate and tropical environments, and increasing floods and droughts and intensive forest fires in sub-polar, boreal, tropical and temperate biomes, all of which have far-reaching impacts on vegetation and its potential to establish and to affect river morphodynamics.	Christensen and Christensen (2003); Nilsson et al. (2005); Moriondo et al. (2006); Cochrane and Laurance (2008); Dufour and Piégay (2009); Diolaiuti et al. (2011); Fan et al. (2020); Grill et al. (2019); Skalak et al. (2013); Piégay et al. (2020); Poff (2014); Kundzewicz et al. (2014); Alencar et al. (2015); Lozano et al. (2017); Janssen et al. (2018); Wohl (2020).
Catchment scale impacts	Rapid changes in land use on floodplains or across entire watersheds strongly modulate hydrosedimentary fluxes, local shear stress and flow resistance, and thus interactions among plants, hydrological and geomorphological processes. For example, in numerous regions of Europe, the discontinuation of agropastoral practices in mountainous areas and floodplains during the late 19 th century and following the Second World War resulted in the spontaneous growth of forests on hillsides and riverbanks. This, in turn, has had direct and indirect impacts on various aspects of channel morphology.	Marston et al. (1995); Bravard et al. (1997); Liébault and Piégay (2002); Erskine et al. (2012); Arnaud-Fassetta and Fort (2014); Surian et al. (2015).
Reach and sub-reach scales impacts	Removal of riparian vegetation along riverbanks and floodplains alters vegetation effects on river morphodynamics. In addition, changes in vegetation health (e.g., caused by channelization processes), can be accompanied by changes in density, biomass, abundance, leaf area, stem flexibility and resistance to breakage, and thus alter vegetation	Gregory and Gurnell (1988); Chambers et al. (1991); Johnson (1994, 2000); Carr (1998); Heaney et al. (2001); Bennett et al. (2002); An et al. (2003); Webb and Leake (2006); Stutter et al. (2007); Tao et al. (2008); Ságová-Marečková et al. (2008); Trimmer et al. (2009, 2017); Jones et al.

Table 3 (continued)

Modulator	Vegetation responses to, and effects on, river morphodynamics	References
	interactions with water flow and sediment transport and, ultimately, its potential to affect channel morphology. For example, reach-scale impacts of water resource exploitation may be a reduction in river flows and/or riparian water table levels, leading to desiccation and a consequent decrease in riparian vegetation vigour and biomass, and changes in species assemblages. Alternatively, an increase or stabilization in river flows and riparian water table levels may lead to a subsequent stability or increase in riparian vegetation growth and biomass. This situation is exacerbated in dryland rivers where flow regulation has modified the flow regime, commonly by producing less peak and more uniform flows.	(2012); Gurnell et al. (2013); Wohl (2020).
	Other anthropogenic effects include the modification of biogeochemical processes and nutrient availability, which modulate the biogeomorphological processes (e.g., when increasing the deposition of fine sediment, which tends to have a high content of biologically available organic matter and inorganic nutrients).	
Direct impacts on flow and sediment fluxes	Along the river continuum, dams and weirs disrupt hydrosedimentary fluxes. Such situations can result in complex flow-sediment-vegetation interactions and biogeomorphological responses.	Schumm (1969); Petts (1979); Brookes et al. (1983); Petts (1984); Erskine (1985); Bravard et al. (1986); Brookes (1988); Johnson (1994, 1998); Marston et al. (1995); Ward and Stanford (1995); Steiger et al. (1998, 2000); Stanford and Ward (2001); Gergel et al. (2002); Baptist et al. (2004); Brierley and Fryirs (2005); Petts and Gurnell (2005, 2022); Graf (2006); Geerling et al. (2008); González et al. (2010); Cooper and Andersen (2012); Dixon et al. (2012, 2015); Garófano-Gómez et al. (2013); Shafroth et al. (2016); Martínez-Fernández et al. (2017); Sanchis-Ibor et al. (2019); Johnson et al. (2015); Adami et al. (2016); Corenblit et al. (2016a, 2020); Bejarano et al. (2018); Aguiar et al. (2018); Serlet et al. (2018); Volke et al. (2019); Janssen et al. (2022); van Oorschot et al. (2022).
	Flood regulation can lead to a phase of strong colonization and encroachment of alluvial bars and floodplains by native or non-native riparian vegetation, resulting in channel narrowing. Vegetation succession develops because the attenuated flow regime, when combined with a common coarse sediment deficit, limits or even impedes vegetation destruction and associated succession rejuvenation. In vegetation-encroached rivers with a bedload deficit, vegetation acts as a strong constructing and stabilizing factor at the reach scale, and leads to channel simplification and potential bed incision.	
	Hydropeaking, i.e., rapid fluctuation of water flow	

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Table 3 (continued)

Modulator	Vegetation responses to, and effects on, river morphodynamics	References
	caused by hydroelectric power station operations, affects plant growth and survival by altering water availability, nutrient content, and sediment dynamics. Vegetation can also be physically damaged by changes in water levels and flow rates. The effects of hydropeaking on riparian vegetation vary depending on the frequency, intensity, and timing of flow fluctuations, as well as other factors such as river morphology and climate.	
	In channelized rivers, the main river channel tends to be artificially disconnected from its floodplain and natural transversal hydrogeomorphological and biogeomorphological interactions are impaired. The effects of vegetation on river morphodynamics are thus impeded at the corridor scale. However, vegetation can still significantly affect in-channel morphodynamics (i.e., within artificial levees) if the channel gradient is sufficiently low and the space between the artificial levees is sufficiently wide for plants to establish on alternate and median bars. Nevertheless, vegetation is generally routinely removed by river management authorities to maintain channel flow conveyance between the artificial levees.	

Fig. 5) is dominated by bare sediment and occurs during alluvial bar formation or following vegetation destruction by floods. The pioneer phase (P in Fig. 5) corresponds to the colonization of bars by seedlings and saplings on newly formed or rejuvenated alluvial bars. The biogeomorphological phase (B in Fig. 5) occurs when pioneer grass, shrubs or trees establish on the alluvial bars within the exposed zones of the active channel and affect hydrogeomorphological processes and fluvial landforms. Finally, the ecological phase (E in Fig. 5) corresponds to the maturation of riparian forests on stabilized and disconnected islands and floodplains. The FBS model intimately links geomorphological and riparian vegetation units in a functional framework where the evolution of the biogeomorphological units is driven by various types of functional linkages associated with plant dispersal, anchorage, stability, resource storage and acquisition, biomass production and recycling, reproduction (i.e., plant responses), and plant effects on fluvial landforms.

The FBS model reflects the evolution of biogeomorphological units, in which vegetation and geomorphology have reciprocal effects, but which generally does not follow a linear trajectory from pioneer to mature successional stages (Fig. 6; Corenblit et al., 2010, 2014). Instead, trajectories are characterized by abrupt changes between alternative stable states and hysteresis cycles (*sensu* Scheffer et al., 2001), as represented by specific sets of interlinked biotic and abiotic conditions where vegetation effects and biogeomorphological feedbacks are either impeded or stimulated (Francis et al., 2009; Corenblit et al., 2014; Stallins and Corenblit, 2018).

Table 4

Biological modulators of vegetation responses to, and effects on, river morphodynamics.

Modulator	Vegetation responses to, and effects on, river morphodynamics	References
Biological controls	Vegetation modulates its responses to, and effects on, environmental conditions within riverine systems at various levels of organization (i.e., individual, population and community) and from instantaneous to evolutionary timescales.	Hupp (1983); Hickin (1984); Hupp and Osterkamp (1985); Nilsson (1987); Pautou and Arens (1994); Tabacchi et al. (2019); Karrenberg et al. (2002); Lytle and Poff (2004); Bornette et al. (2008).
Morphological reconfiguration in stream flow	Riparian plants are regularly exposed to drag forces related to flowing water at different scales, ranging from the leaves, branches, stems, single plants, plant units, and mosaic of plant units. During a single flood, plants instantaneously reconfigure the morphology of their aerial structures (i.e., stems, branches and leaves) in response to stream flow. Pioneer riparian woody plants bend and streamline their above-ground biomass in response to hydraulic forces. Morphological reconfiguration in flowing water has been interpreted as a direct response to shear stress in order to minimize drag force and thus limit the risk of plant breakage and uprooting. The presence of flexible plants within the flow affects local hydraulic properties and sediment dynamics according to the morphological reconfiguration in the fluid.	Usherwood et al. (1997); Gom and Rood (1999); Tsujimoto (1999); Beismann et al. (2000); Nepf and Vivoni (2000); Dodds (2002); Järvelä (2002); Boller and Carrington (2006); James et al. (2008); Nikora (2010); Puijalón et al. (2011); Stone et al. (2013); Albayrak et al. (2014); Västilä and Järvelä (2014); Kui et al. (2014); Manners et al. (2015).
Phenotypic plasticity	Phenotypic plasticity, and potentially epigenetics, is the capacity of one genotype to produce a set of phenotypes (i.e., norms of reaction) in a fluctuating environment. Phenotypic plasticity may be a key process by which plants cope with fluctuating environmental conditions unrelated to seasonality, and it concerns all morphological, physiological and phenological characteristics that interact with the environment. Over several seasons and years, certain plant species can provide plastic responses in relation to the interaction between their genotype and the environment, particularly to regular mechanical constraints and physiological stress. Mechanical constraints, in particular, are imposed on plants during floods by shear stress and sediment burial. Between floods, physiological constraints such as	Stromberg and Patten (1990); Shafroth et al. (1998); Bellingham and Sparrow (2000); Johnson (2000); Rood et al. (2000); Scott et al. (2000); Shafroth et al. (2000, 2010); Willby et al. (2000); Guillois-Froget et al. (2002); Kozłowski and Pallardy (2002); Li et al. (2005); Day et al. (2006); Stella et al. (2006); Anderson and Mitsch (2008); Puijalón et al. (2008); Dufour and Piégay (2008); Meier (2008); Rodríguez-González et al. (2010); Bornette and Puijalón (2011); Puijalón et al. (2011); Herbison et al. (2015); Stromberg and Merritt (2016); Kui and Stella (2016); Garófano-Gómez

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Table 4 (continued)

Modulator	Vegetation responses to, and effects on, river morphodynamics	References
	water deficiency can also impede vegetation development. Canopy height, volume and architecture of aerial plant parts, as well as the depth and architecture of roots, have all been identified as showing highly plastic responses to hydrogeomorphological changes.	et al. (2016); Bourgeois and González (2019); Schook et al. (2020).
	Phenotypic plasticity also concerns physiological and phenological characteristics. For example, in semi-arid contexts, poplars commonly experience branch die-back (branch sacrifice), which was interpreted as a physiological adaptation to maintain the plant's water balance when less water is available during droughts, reductions of flow discharge, or water table declines. The duration and period of seed release of poplar/cottonwoods and willows also vary according to climatic and hydrological conditions, typically synchronizing with floods that produce the bare and moist alluvial surfaces required for their recruitment.	
Seasonal phenology	Vegetation biomass, surface cover and morphology generally vary greatly between seasons, leading to changes in surface roughness in fluvial corridors, which is important in controlling river morphodynamics.	Manning (1891); Cowan (1956); Shih and Rahi (1982); Sand-Jensen (1997); Tabacchi et al. (2000); Järvelä (2002); Cranston and Darby (2004); Cotton et al. (2006); Heppell et al. (2009); Kleeberg et al. (2010); Canham et al. (2012); Politti et al. (2018).
	Leaves are a major contributor to the drag of a plant within a fluid. Manning's <i>n</i> significantly increases in community patches during the leafy vegetative period. Thus, the hydraulic and hydrogeomorphological impact of vegetation during floods can vary enormously with the seasonal timing of the flood.	
	At the water table, seasonal cycles of root growth, with drawdown in the warm season followed by trimming in response to water table rise in winter, occur in phreatophyte plants. This response in seasonally water-limited environments ensures that plants have access to groundwater throughout the year and increases sediment cohesion.	
Vegetation succession and introduction of non-native plants	Over several decades or centuries, plant species assemblages vary in relation to biological interactions (e.g., facilitation and competition) and changes in the hydrological/sediment regime and/or habitat conditions.	Turner (1974); Graf (1978); Everitt and Graf (1979); Carman and Brotherson (1982); Bravard et al. (1986); Pautou et al. (1997); Mack and D'Antonio (1998); Tabacchi et al. (2000); Stevens et al. (2001); Gage and
	River structure and function can be extensively and durably	

Table 4 (continued)

Modulator	Vegetation responses to, and effects on, river morphodynamics	References
	changed when non-native plant species are introduced, particularly when the new invasive species can resist small to intermediate floods and/or recover after large floods.	Cooper (2005); Steiger et al. (2005); Birken and Cooper (2006); van Pelt et al. (2006); Bornette et al. (2008); Stromberg et al. (2009); Merritt et al. (2010); Cadol et al. (2011); Fei et al. (2014); Garófano-Gómez et al. (2017); Butterfield et al. (2020).

The balance between destructive and remobilizing forces related to the hydrogeomorphological disturbance regime, and stabilization and constructive forces related to substrate cohesion and vegetation, bounds the stable ecological and geomorphological domains (Francis et al., 2009; Corenblit et al., 2014). Critical factors thus include the duration, frequency and magnitude of floods and bedload transport *versus* the establishment and growth performance of engineer plants, and the proportions of plants, logs (large wood), and sediment particle sizes to channel size. Changes in flood intensity and frequency, the construction of a dam that impedes flow variability and sediment continuity, or the introduction of an invasive non-native plant engineer species with alternative ecological characteristics, may all cause bio-geomorphological thresholds to be crossed along environmental river gradients (Johnson, 1994; Piégay et al., 2020; O'Briain et al., 2023). Under such circumstances, the pattern of relationships between higher levels of organization (mosaic of communities and geomorphological units at the reach scale) and lower levels of organization (individual plants and sediment tails; pioneer community and pioneer landform) are modified, and rapid bottom-up and top-down cascade effects can occur through the entire fluvial corridor (Corenblit et al., 2010; Larsen, 2019).

Cascade effects potentially result in new stable geomorphological and ecological domains, dominated by either physical or biological processes, at the corridor scale (Fig. 6: G-P or E phases, respectively) (Schumm, 1969; Fisher et al., 2007; Stallins and Corenblit, 2018). For example, an increase in sediment delivery and frequency of high-magnitude floods over a few years or decades can lead to a sharp transition from a relatively stable meandering fluvial style towards a relatively unstable wandering, island braided or braided style (Beschta, 1983; Métivier and Barrier, 2012). In contrast, a decrease in flood frequency and magnitude can result in bottom-up cascading effects of vegetation establishment, growth and aggregation that lead to afforestation and stabilization of the entire fluvial corridor (e.g., from P/B to E in Fig. 6) (Nadler and Schumm, 1981; Johnson, 1994, 1998; Graf, 2006; Stecca et al., 2019). Between these two opposite states, respectively dominated by bare substrate and pioneer plants or disconnected riparian forests with mature trees (in temperate and tropical regions), an array of patchy, shifting configurations of pioneer and post-pioneer islands can be the expression of metastable states, where discrimination between vegetation responses and effects becomes challenging (Francis et al., 2009; Gurnell et al., 2012).

The aforementioned models help to consider vegetation as a potential major driver of river morphodynamics and contextualize processes and key factors, but they cannot resolve the difficulties of formally disentangling plant effects from physical controls above the local scale (i.e., individual plant to patch scale; ca. 10^{-1} - 10^2 m). Even if these conceptual models have proved to be useful, they do not enable informative exploration of the larger spatiotemporal scales and/or alternative contexts where it is difficult to distinguish the effects of vegetation on river morphodynamics from other physical drivers. Great care is

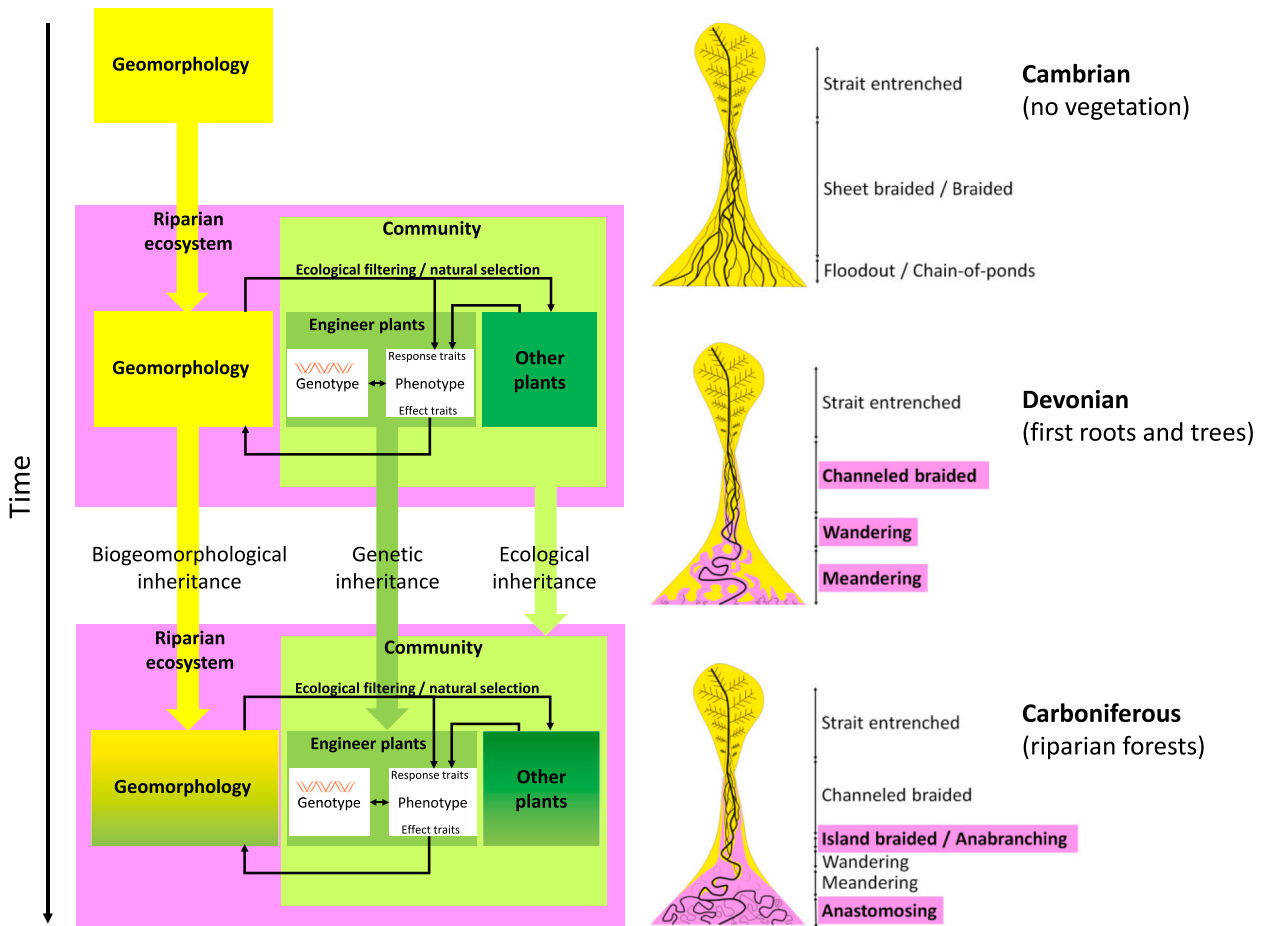


Fig. 2. Conceptual model of river biogeomorphological dynamics as a complex adaptive system that has emerged and evolved following land colonization by plants in the Late Ordovician (modified from Corenblit et al., 2014, 2021). The yellow box represents the geomorphological environment. The riparian ecosystem is represented in pink. The green box represents the species community with the engineer plant species (in olive green) and the other companion plant species present in the ecosystem (in darker green). Geomorphological and biological changes related to niche construction (for a detailed explanation of the concept, see Corenblit et al., 2021) are represented with the green colour gradient. The arrows represent two possible types of interaction: (i) ecological filtering of species and species traits with organismal activity affecting community structure and function; and (ii) natural selection, where organismal activity impacts the selection pressures and drives the evolution of the engineer species itself or other species. The different sources of inheritance in the complex adaptive system (i.e., biogeomorphological, genetic and ecological) are indicated. The new river styles associated with plant effects are indicated, with the most common river styles occurring in each period at the basin scale highlighted in pink colour.

needed when attempting to generalize from these models because vegetation does not systematically play the dominant role in river morphodynamics, and also because scaling up plant effects observed at local scales (individual to pioneer island) to larger scales (river reach) is not straightforward.

4. Significance of plant effects: a matter of spatiotemporal scales along the longitudinal energy and resource gradients

The nature and significance of vegetation effects on river morphodynamics vary across spatiotemporal scales and levels of biogeomorphological organization (Figs. 7 and 8; Gurnell et al., 2012). Vegetation can affect hydrogeomorphological processes and landforms from the very local scale — for instance, a small individual plant creating a dissipative structure in the flow that may lead to the development of a centimeter- to multiple meter-size sediment tail during a single flood event (Rodrigues et al., 2007; Schnauder and Moggridge, 2009; Euler et al., 2014; Corenblit et al., 2016b) — to community mosaic effects on reach-scale, channel-floodplain development during decades, centuries and millennia of vegetation succession (Salo et al., 1986; Gurnell and Petts, 2002; Tooth et al., 2008; Gurnell, 2014; Larsen, 2019). Therefore, the criteria for defining the significance of vegetation

effects on river morphodynamics vary conceptually and practically according to the spatiotemporal boundaries that are determined by the observer. Whereas vegetation effects at short time (ca. 10^{-1} - 10^1 years) and local scales (ca. 10^{-1} - 10^2 m) are easier to validate statistically and empirically, larger scales are far more challenging, in part due to the finite length of instrumental records (Larsen et al., 2021).

The formation of a well-defined centimeter- to multi-meter-scale sediment tail downstream of a living individual plant, a small vegetated patch or a wood jam during a flood within a high energy braided active channel (Fig. 9) — for instance, with a specific stream power at bankfull of $>300 \text{ W m}^{-2}$ (after Nanson and Croke, 1992) — could be considered a significant effect at the local scale over days or a few months. However, it is not considered a significant effect at the reach scale over few years or decades if the sediment tails do not become coalescent or result in the recruitment of new individuals.

Indeed, in highly disturbed and unstable straight confined and braided gravel-bed rivers, local short-lived sediment tails that form downstream of isolated shrubs or patches do not quickly enlarge and/or coalesce into larger features. These features only represent ‘noise’ at the reach scale and are not able to have cumulative organizational impacts on the larger scales of river morphodynamics (B style in Fig. 8). In high-energy braided river reaches, such as the Tagliamento River, threshold

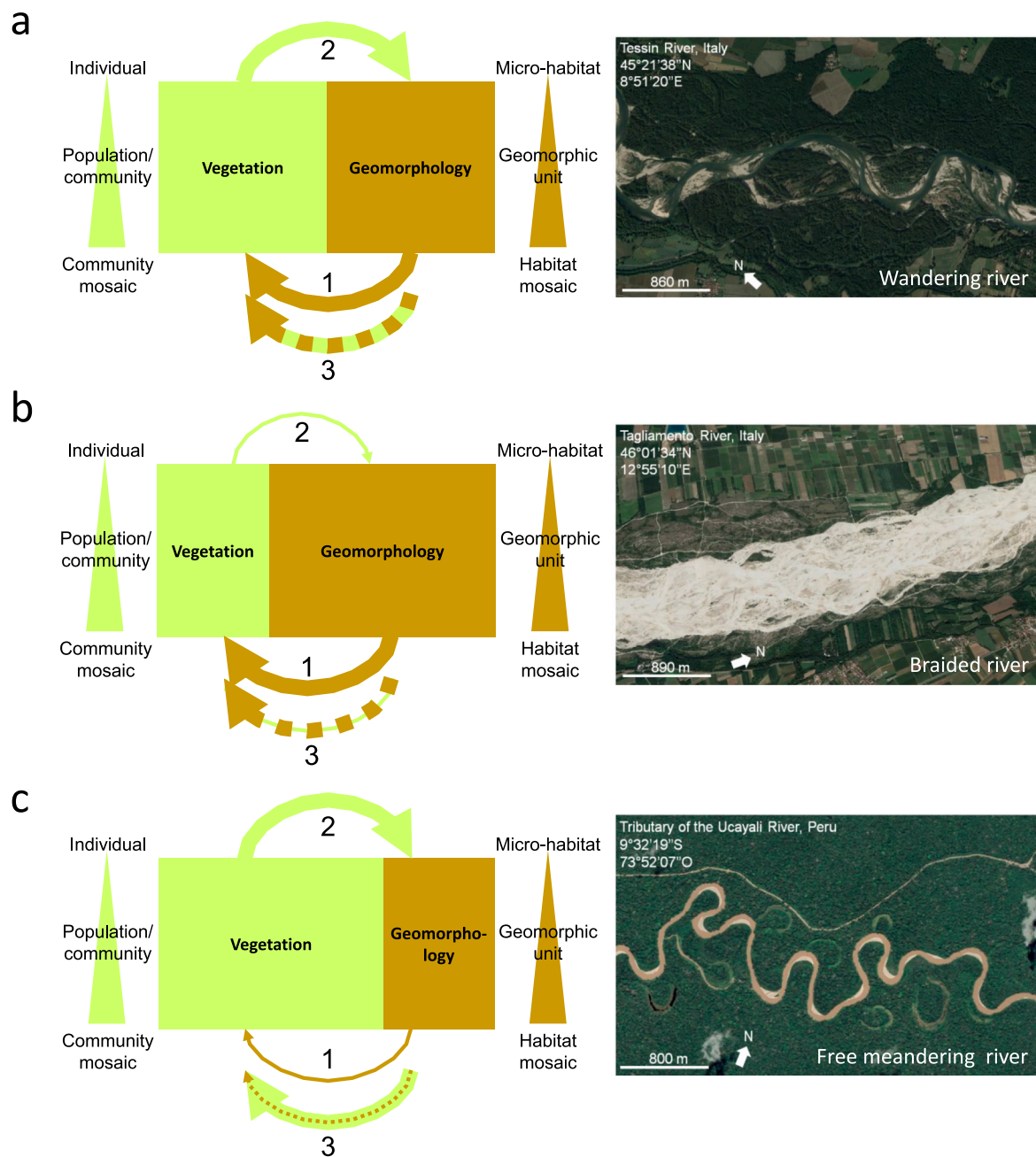


Fig. 3. Simplified model of interactions between vegetation and geomorphology. The main levels of biological and physical organization are indicated by the triangles on either side of the model. The width of the arrows represents the importance of each factor in the feedback. Arrow 1 in brown: initial effect of geomorphology on vegetation; arrow 2 in light green: vegetation effect on geomorphology; arrow 3 in dashed light green-brown: feedback of the modulated geomorphologic environment on vegetation. a) shows a system dominated by feedbacks between vegetation and geomorphology (Tessin River, Italy; temperate biome); b) shows a system dominated by physical forcing (water flow and sediment transport) (Tagliamento River, Italy; temperate biome); and c) shows a system dominated by the effects of plants on river morphodynamics (Ucayali River, Peru; tropical humid biome). The structure of the interaction may also be transformed as a function of changes in the hydrosedimentary regime, the biological setting (e.g., invasion by an exotic plant species) or the anthropogenic context (e.g., construction of a dam). Aerial photographs taken from Google Earth™.

discharges and/or range of discharges exist, above which the removal of vegetated patches within the active channel becomes dominant (Surian et al., 2015). Combined with high stream power, low alluvial moisture and low nutrient availability in the coarse sediments of straight confined or braided river reaches lead to lower vegetation growth. Decreased growth, in turn, leads to easier removal of developing vegetation patches, reinforcing the impediment of vegetation development related to the balance between the disturbance regime and plant growth rates. For example, Bätz et al. (2016) showed on the Allondon River, Switzerland, that groundwater upwelling favours vegetation growth,

permitting riparian trees to quickly enhance channel stability and reduce active channel width. By contrast, where groundwater is downwelling, vegetation cover remains patchier, plant effects are reduced, and a wider but bare active channel is maintained. Similar groundwater level effects on vegetation dynamics were observed on the Tagliamento River by Bertoldi et al. (2011b).

Small biogeomorphological structures remain crucial to initiating vegetated landforms. They are a critical part of vegetated landform development over larger areas and longer time periods in downstream (less energetic) reaches, where positive feedbacks of landform accretion

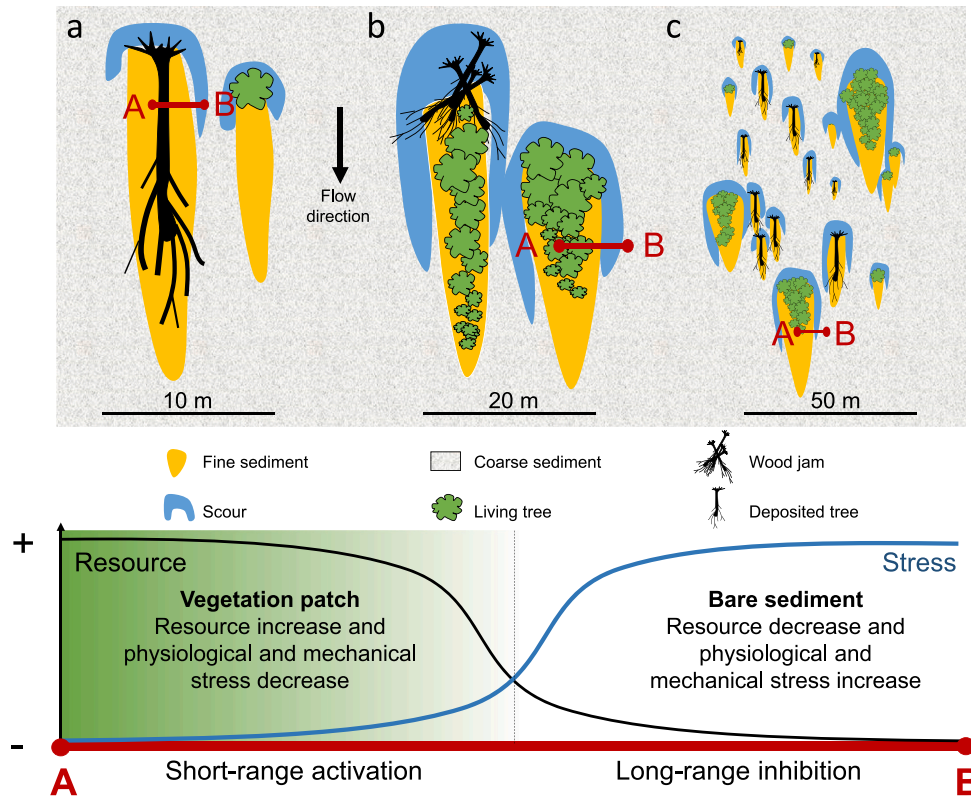


Fig. 4. Scale-dependent feedback model applied to vegetation effects across a river bed. Adapted from Gurnell et al. (2005).

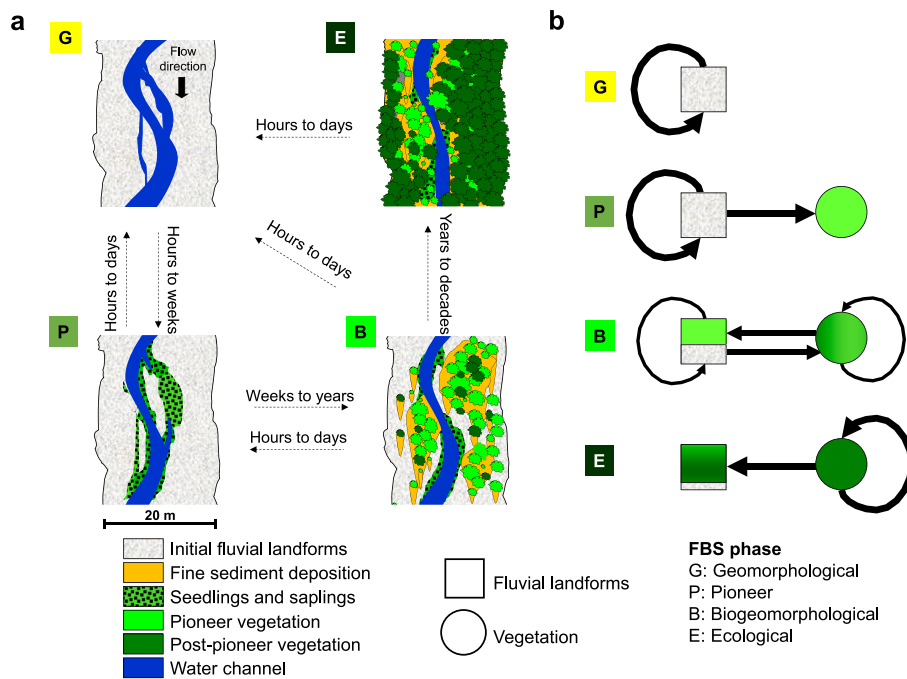


Fig. 5. The Fluvial Biogeomorphological Succession (FBS) model. a) details of each phase and the time frame of transitions between phases; b) feedbacks within and across geomorphological and ecological processes, with arrow weights representing the importance of each relationship during that phase. The squares represent the physical compartment and the circles the biotic compartment. The grey colour corresponds to abiotic factors and the green colour to biota. Modified from Corenblit et al. (2009b).

and vegetation growth can occur (Gurnell et al., 2001, 2005; Rodrigues et al., 2006; Bertoldi et al., 2011a). We suggest that vegetation effects on river morphodynamics can become significant at the reach scale when landform resistance and surface roughness are modified in such a way

that at least one key variable describing channel planform geometry (e.g., braiding index and degree of sinuosity, wavelength, amplitude and radius of meanders), transversal geometry (e.g., channel width, depth, width/depth ratio), or sediment texture (e.g., mean, median, mode,

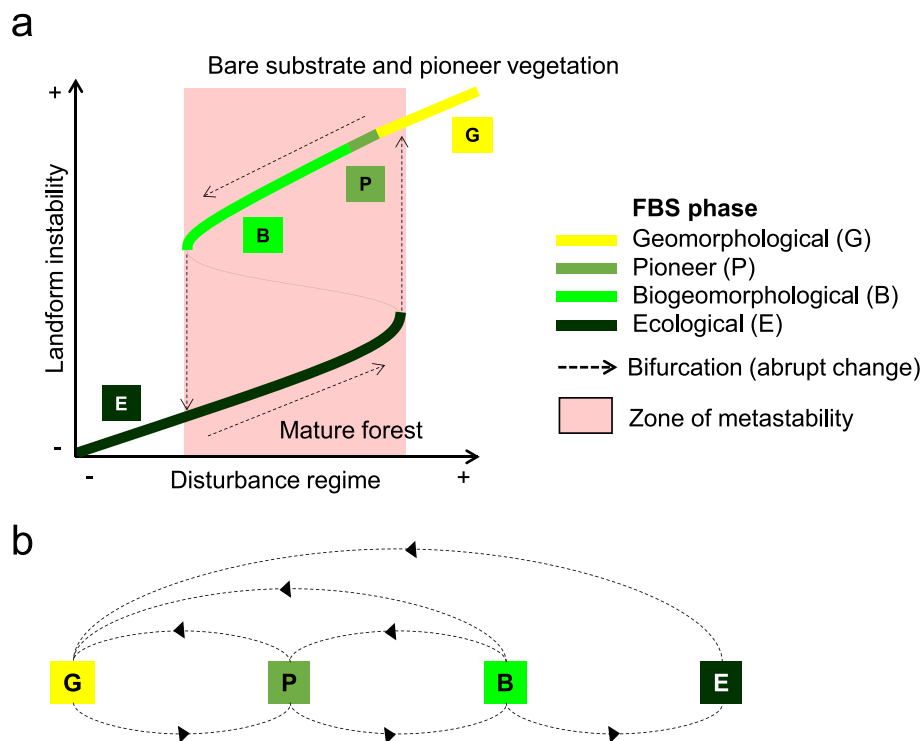


Fig. 6. Conceptual non-linear model of fluvial landform instability during the Fluvial Biogeomorphological Succession (FBS; see Fig. 5 for description): a) model of a hysteresis cycle (*sensu* Scheffer et al., 2001) in landform instability according to the responses and effects of riparian vegetation during the FBS; b) FBS model, with each potential transition between phases shown in Fig. 5. See Corenblit et al. (2010) for a practical illustration of successional transition probabilities calculated on the Tech River, France.

standard deviation, skewness, kurtosis), is significantly and durably changed.

In the temperate biome, Gurnell and Bertoldi (2020) showed how vegetation can initiate a positive feedback of landform and vegetation growth on a braided reach of the Tagliamento River. They pointed out that in river reaches where the disturbance regime is high, a sufficiently rapidly growing, robust patch of vegetation is required to initiate the cycle of biogeomorphological construction. The island model of Gurnell et al. (2001) considers three possible starting points for vegetation on an exposed bare surface: (i) dispersed seeds/small vegetative propagules on open, coarse, free-draining sediment surfaces; (ii) seeds/small vegetative propagules retained with finer moisture-retentive sediments within/behind a physical obstacle (e.g., a dead wood pile); and (iii) seeds/small vegetative propagules retained with finer moisture-retentive sediments within/behind a rapidly sprouting large vegetative propagule. Any of these local biogeomorphological configurations could initiate landform development once the vegetation is able to establish sufficiently quickly to survive local disturbances (e.g., when species of the Salicaceae family establish; González et al., 2018). Although specifically developed with observations from the Tagliamento River in island braided reaches (IB style in Fig. 8), the island model remains relevant for any alluvial river, whereby propagules might be able to survive sufficiently long to have the chance of contributing to the initiation of landform development in some intermediate to low energy locations (Francis, 2006; Francis et al., 2009; Moggridge et al., 2009; Picco et al., 2017; Gurnell et al., 2018; Gurnell and Bertoldi, 2020). As flow energy increases, larger or more clustered and/or more rapidly growing vegetation patches may be required to initiate positive feedback and drive the system toward aggraded and stabilization states at the scale of large patches or the scale of the fluvial corridor (Han and Brierley, 2020; Henriques et al., 2022).

Many studies have shown that biogeomorphological feedbacks leading to cumulative effects across spatiotemporal scales are generally maximized at the intermediate to the low spectrum of the longitudinal

energy gradient. This is particularly the case in river reaches of any size that are characterized by moderate bedload transport combined with sand- and silt-grade sediments; for instance, with a specific stream power at bankfull of 10–200 $W m^{-2}$ (after Nanson and Croke, 1992) (Corenblit et al., 2014). In such instances, the effects of vegetation can be significant (across spatiotemporal scales) if sediment tails forming downstream from young individuals on alluvial bars are not systematically eroded during floods, and are able to coalesce and evolve from vegetated ridges or patches (dominated by young trees over few years) to pioneer and mature vegetated fluvial ridges, islands and benches (over a few decades to centuries). Over multiple decades to centuries, vegetation development can even contribute to the building of extensive forested floodplains in piedmont zones and lowlands, such as those associated with wandering (W style in Fig. 8) and meandering river styles (M style in Fig. 8).

Reciprocal interactions between geomorphology and plants can also occur at the largest spatial scales over centuries and millennia. Large fluvial islands and floodplains in low energy reaches — for instance, with a specific stream power at bankfull $<10 W m^{-2}$ (after Nanson and Croke, 1992) — develop from the reciprocal coupling between floodplain forest dynamics and fluvial processes, leading to the formation over millennia of extensive floodplains and deltas with anastomosing fluvial styles (A style in Fig. 8) (Smith, 1976; Salo et al., 1986; Hupp, 2000; Friedrichs and Perry, 2001; Makaske, 2001; Tooth et al., 2008).

5. Current challenges to disentangle abiotic-biotic cause and effect relationships above the local scale

It is now well understood that vegetation within riverine systems responds and adapts to the fluvial disturbance regime (Karrenberg et al., 2002; Lytle and Poff, 2004; Bornette et al., 2008; Corenblit et al., 2015). However, above the local scale, it remains challenging to identify and quantify the combined above- and below-ground vegetation effects on morphodynamics and river styles, and to separate them from

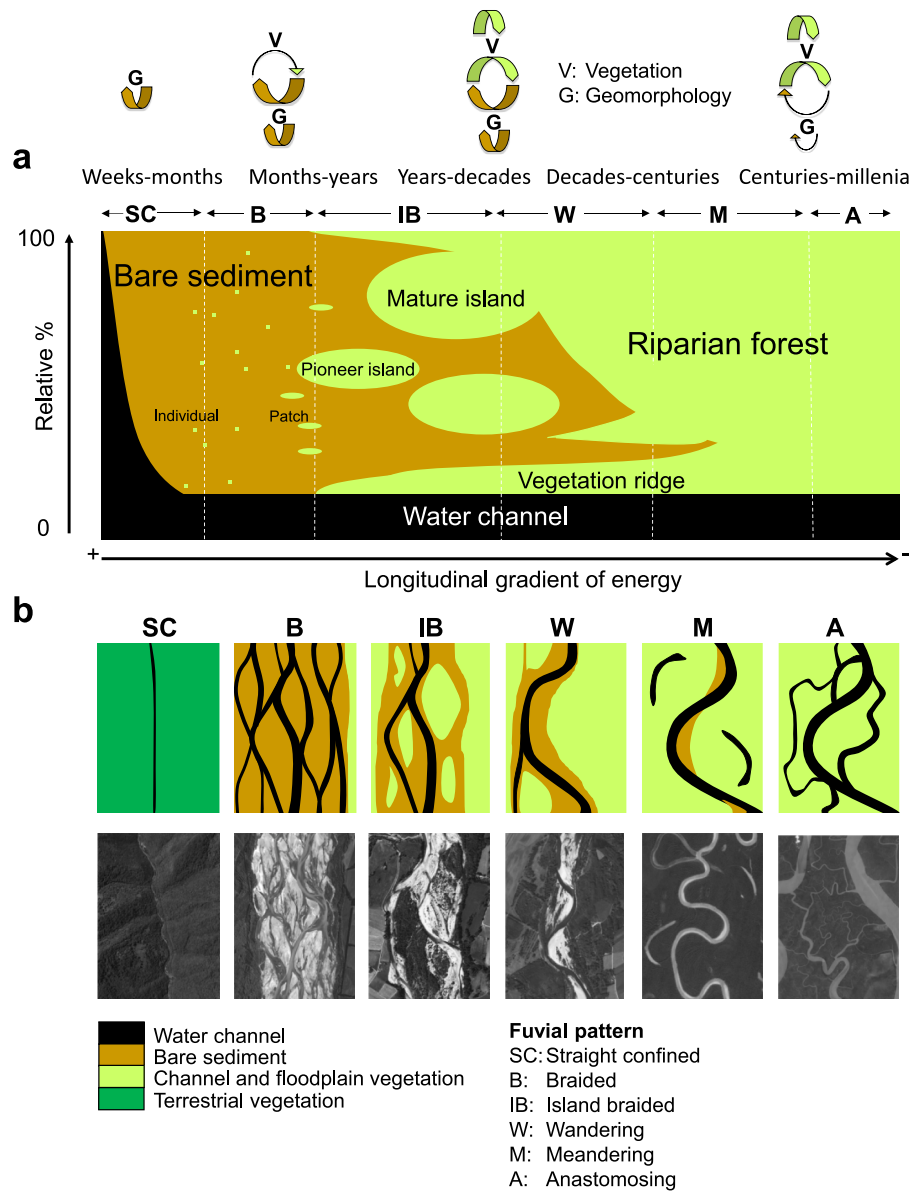


Fig. 7. Conceptual model of: a) vegetation effects across spatiotemporal scales and along the longitudinal (upstream-downstream) energy gradient (left to right); and b) distinguishing between different fluvial styles within humid temperate and tropical biomes.

hydrogeomorphological controls and river adjustments.

The significance of an effect can be defined objectively using formal criteria that can be adjusted according to the required degree of precision of a prediction (Kanji, 2006). We suggest that the effects of vegetation on river morphodynamics are meaningful if they result, at a given spatiotemporal scale, in permanent or recurrent geomorphological dynamics or structures (e.g., related to channel migration and bank erosion rate and width-depth ratio, alluvial bar stability, texture and elevation, floodplain accretion rate, or landscape heterogeneity and complexity) that can be directly attributed to vegetation through statistical deviation from their equivalent abiotic state. However, for all scales larger than the local, the power of statistical predictions can be limited practically by the fact that other physical drivers (in concert with vegetation) shape biogeomorphological patterns (see Kleinhans et al., 2023).

Flume experiments (e.g., Tal et al., 2004; Tal and Paola, 2010) that seek to isolate vegetation controls on river morphodynamics may be problematic because complex field conditions are not completely reproducible (Bertoldi et al., 2015; Mao et al., 2020). It is challenging to uniformly scale down plant physiology and dimensions (relative to grain

size), and replicability can be an issue as finding two identical reaches or river systems is virtually impossible. Furthermore, coexisting factors can co-vary without direct linkages between them, so correlations between vegetation and river geomorphological features should be viewed and analysed with caution (Corenblit et al., 2019, 2020). Differences between control and impact sites can be much more complex than in idealized representations. If an observed geomorphological state (e.g., defined by topographic elevation, landform stability and sediment texture) co-varies with vegetation structure and dynamics (e.g., vegetation surface cover, mean stem height, mean stem diameter and density, biomass and its temporal variation), unequivocal differentiation of vegetation responses to, and effects on, river morphodynamics remains problematic.

5.1. Vegetation and meandering rivers

The physical dynamics of meander formation (e.g., Bolla Pittaluga and Seminara, 2011; van Dijk et al., 2013b) traditionally have been considered by river scientists as the main driver for riparian vegetation

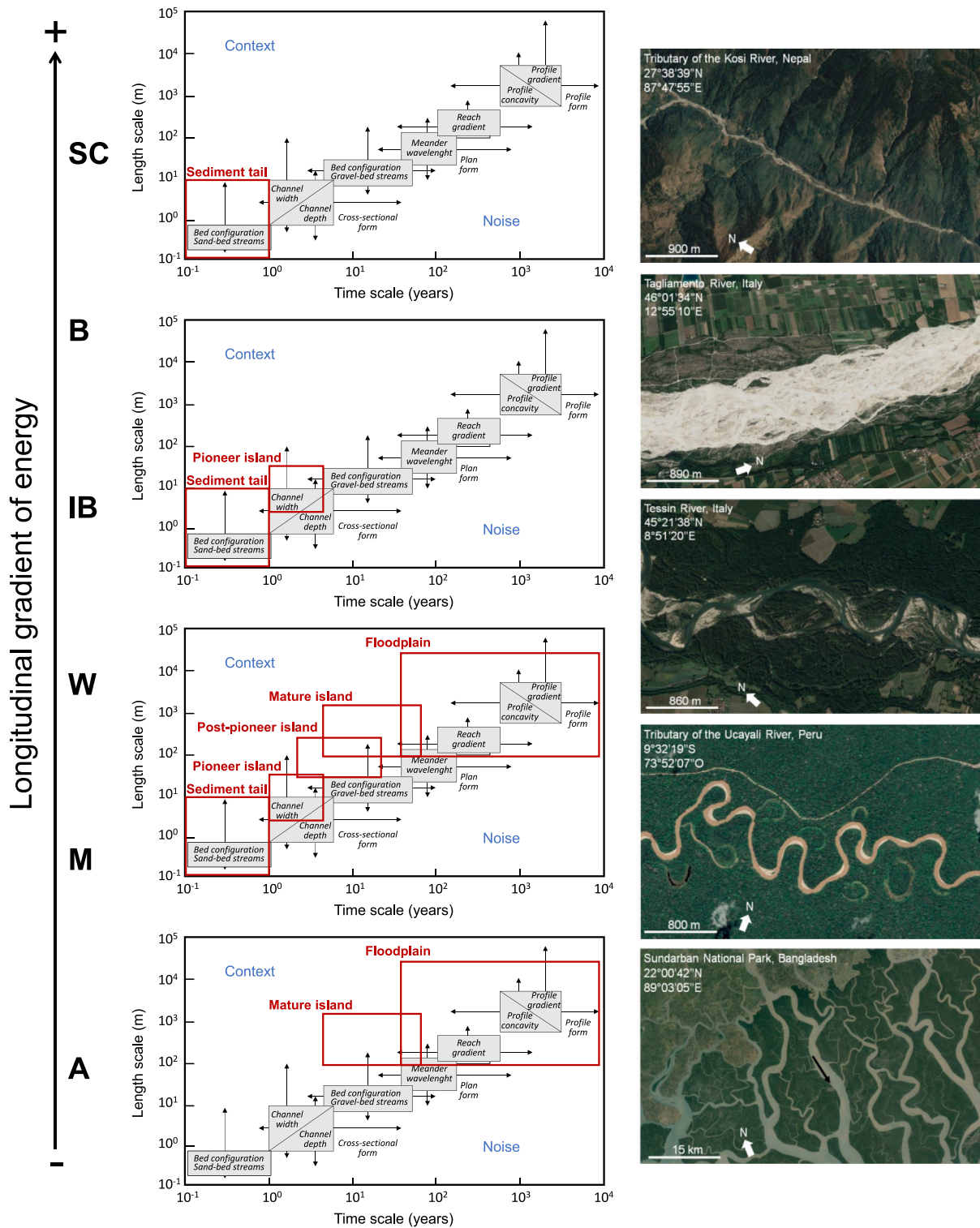


Fig. 8. Spatiotemporal expression of plant effects across spatiotemporal scales and along the longitudinal (upstream-downstream) energy gradient (adapted from Knighton, 1998). The grey boxes indicate geomorphological characteristics and the red boxes indicate biogeomorphological units along a gradient of size and maturity. Aerial photographs taken from Google Earth™. Fluvial style SC: straight confined, B: braided, IB: island braided, W: wandering, M: meandering; A: anastomosing.

spatial organization and dynamics (Hickin and Nanson, 1975; Johnson et al., 1976; Junk et al., 1989; Kalliola et al., 1991, 1992; Pautou et al., 1997). However, the dynamics of meandering itself have also been considered as being fundamentally related to vegetation to the extent that the two aspects of fluvial systems should be considered in conjunction (e.g., Kyuka et al., 2021; Ielpi et al., 2022). Ongoing debates

still discuss the exact functional status of vegetation as a response to, and as an effect on, river meandering (Kleinhans et al., 2023).

Liébault and Piégay (2002) and Dufour and Piégay (2009) showed, from the freely meandering Ain River, France, that channel narrowing occurred one to two decades before dam construction lowered peak flows and interrupted sediment transport downstream. This narrowing



Fig. 9. Well-defined, meter-scale sediment tails forming downstream from small, isolated poplar resprouts in the highly dynamic active channels of the Durance River, France (Mediterranean temperate biome). The size and volume of the sediment tails may be related to the volume of the plants and flow characteristics (i.e., height, velocity and transported sediment) during a flood. Photograph: D. Corenblit.

was synchronous with spontaneous afforestation of the floodplain as a consequence of grazing decline. Liébault and Piégay (2002) also showed that the meandering Doubs River, France, did not undergo narrowing while grazing activity continued. Likely, land-use changes in the Ain fluvial corridor, from grazing to a largely grazing-free, dense riparian forest, may explain an overall increase in floodplain resistance to erosion. In addition, the drivers of meander dynamics changed from chute cutoff to neck cutoff, and there were longer cycles of floodplain renewal, as well as changes in vegetation succession and in the resulting vegetation patch mosaic. However, it is still difficult to appreciate if narrowing and meander dynamics are dominantly related to changes in hydraulic conditions or to vegetation encroachment following grazing decline.

Using a global analysis of free meander migration rates in vegetated and sparsely vegetated rivers from arid regions, Ielpi and Lapôtre (2020) suggested that vegetation is not required for meander formation in all situations, but it might be required where there is no cohesive material to enable bank stability. All other factors being equal, unvegetated meanders migrate an order of magnitude faster than vegetated meanders (see also Schumm, 1968; Ielpi et al., 2017, 2022; Ielpi, 2018; Lapôtre et al., 2019; Ielpi and Lapôtre, 2020). The influence of vegetation on meandering rivers has also been explored through flume tank models. Braudrick et al. (2009) showed that finer sediment and elevated bank strength resulting from vegetation growth are the necessary ingredients for successful meandering in some coarse-bedded rivers. In addition, controlled flume studies have indicated contrasting morphodynamic patterns with and without vegetation (Tal and Paola, 2007; van Dijk et al., 2013a; Vargas-Luna et al., 2019). For example, Kyuka et al. (2021) investigated the effects of vegetation on the evolution of a meandering channel from flume experiments. They showed that the presence of bank vegetation (alfalfa sprouts) maintained a deep, single-thread channel and a limited sediment storage capacity, whereas an unvegetated scenario led to channel widening and high sediment storage capacity. These observations lead to the conclusion that vegetation is not always necessary for the formation of meanders but that it may represent an additional strong control factor modulating meander dynamics and

shape (see review in Ielpi et al., 2022). Ultimately, vegetation may be considered Insufficient but Non-redundant parts of Unnecessary but Sufficient (INUS) conditions (see Illari and Russo, 2014) for meandering patterns, along with aspects of floodplain properties and upstream channel dynamics (which themselves comprise attributes within which vegetation can play an additional INUS role) (Kleinhans et al., 2023).

5.2. Vegetation and island braided and wandering rivers

The debate about the essential role of vegetation in shaping river morphology also continues in the case of island braided and wandering rivers. By using alfalfa at different life stages in a flume experiment, Fernandez et al. (2021) demonstrated that vegetation enhanced the development of new channels, increased channel width, and enhanced topographic variability. However, river morphodynamics were less sensitive to variations in flood discharge as the strength of vegetation influence increased. Overall, sediment transport was reduced under the full-grown vegetation stage, but the presence of mature vegetation on the braid bars resulted in the greatest channel scour depths.

Numerical modelling of vegetation effects on river morphodynamics produces similar results to flume experiments (Camporeale et al., 2013; Nicholas, 2013; Solari et al., 2016; van Oorschot et al., 2016). For example, Crosato and Saleh (2011) used a 2D morphodynamic model with sub-models for flow resistance and plant colonization to show that the variation in vegetation density produced different river patterns. With bare sediment (no vegetation), the river systematically developed a braided pattern, even with a constant discharge remaining below bankfull. With the highest vegetation density, water flow concentrated in a single channel and tended to form meanders. Lower vegetation density led to a transitional geomorphological style, with a low degree of braiding and distinguishable incipient meanders.

Empirical field observations by Bertoldi et al. (2011a) could be consistent with the flume and numerical approaches described above, but transposition of model results to the real world is problematic due to singularities of field conditions, including plant diversity. Bertoldi et al. (2011a) showed that the distribution of bed elevation frequencies in the

active braided channel of the Tagliamento River was associated with vegetation colonization along a transition from bar braided to island braided river patterns. These authors showed that skewness and kurtosis of the bed elevation frequency distribution were correlated with vegetation cover, canopy height, median topographic elevation and growth rate. Such a pattern was also observed in the wandering Allier River, France, for bed elevation and canopy height (Hortobágyi et al., 2017) (Fig. 10).

Bertoldi et al. (2011a) and Hortobágyi et al. (2017) interpreted this as a topographic signature of vegetation development, reflecting sediment trapping and binding within the vegetated patches. However, these case studies highlighted associations but could not formally prove causation. Confounding factors are possible at local scales for explaining topographic variability; for example, in-channel living or dead wood can contribute to island formation, but it does not mean all fluvial islands are originated by in-channel woody vegetation (see also Osterkamp, 1998). Other physical obstacles such as topographic discontinuities can also promote island development, as reported by Rápple et al. (2017). Furthermore, in certain cases, topographic variability associated with vegetation only reflects a response pattern of vegetation establishment and growth owing to localized reduced shear stress and/or better habitat conditions, rather than an effect (Belletti et al., 2014). It is also possible to argue that progressive channel narrowing and deepening can be associated with sediment supply reduction alone, with vegetation gradients being a response to change in morphodynamics rather than an effect on morphodynamics, as illustrated by the theoretical model of Surian and Rinaldi (2003).

Belletti et al. (2013, 2014) hypothesized that the main biogeomorphological island braided gradient (i.e., defined through the presence, the amount, and the relative size of vegetated islands) is based on: (i) the combined effect of their position along the river network (i.e., river gradient, relative elevation, and sediment regime); and (ii) the time since the last large flood (i.e., the recent flood history). Their results showed that even if the regional context (mainly climate and sediment regime) plays a key role, the temporal factor, represented by recent flood history, seems to heavily influence the channel width and vegetation recovery patterns. Based on a space-time comparative approach of a set of braided reaches, Belletti et al. (2014) showed that a clear regional differentiation of riverscape responses could be observed between south-western and south-eastern reaches in the French Alps. This

differentiation depends on several co-occurring factors (i.e., flood characteristics, human impacts, and the climate that controls vegetation dynamics). This example illustrates how vegetation may modulate the morphodynamics of braided rivers while it is modulated itself by other control factors, such as climate conditions, and thus may not necessarily be the overall critical driver.

5.3. Vegetation and anastomosing and anabranching rivers

The anastomosing fluvial style has long been recognized as a distinctive morphology compared to other styles, such as braided and meandering rivers (Leopold and Wolman, 1957; Schumm, 1968; Miall, 1996; for a comprehensive review, see Makaske, 2001). Unlike the latter styles, the influence of vegetation on river morphodynamics in anastomosing rivers is unequivocal because the style is characterized by a stabilized floodplain and a channel avulsion dynamic primarily controlled by vegetation and large wood, at least in humid climates. Several studies have been undertaken into the significant role of vegetation in anastomosing rivers across various spatial scales, biomes and climatic regions, with key case studies including the Okavango Delta in Botswana (e.g., Smith, 1976; McCarthy et al., 1992; Ellery et al., 1993; Stanistreet et al., 1993; Knighton and Nanson, 1993; Makaske, 2001; Gradziński et al., 2003). However, even in the case of anastomosing rivers that correspond to the definition of high-sinuosity (>1.5), multi-channel rivers (Rust, 1978), other physical factors such as slope gradient, hydrology, sediment dynamics, and intrinsic bank cohesion may provide explanatory power in certain contexts (see also Makaske, 2001). For example, Rust (1981) observed the presence of a large, ephemeral, multi-channel fluvial system (Cooper's Creek in the Lake Eyre Basin of central Australia), which he interpreted as a combination of relict braids and active anastomosing channels in an arid context. Here, bare or sparsely vegetated floodplains give rise to the possibility that vegetation was not necessarily fundamental to the formation of this river style. However, as can be seen on Google Earth™, at different dates between 1984 and 2020, the whole river corridor can be dry and bare or sparsely vegetated (e.g., 2009: Fig. 11a), or wetter and better vegetated (e.g., 2010: Fig. 11b), which complicates the analysis of the vegetation as a response or a driver for this river style.

Sub-humid and semi-arid tropical and sub-tropical climates encompass a diverse array of fluvial styles worldwide, corresponding in certain

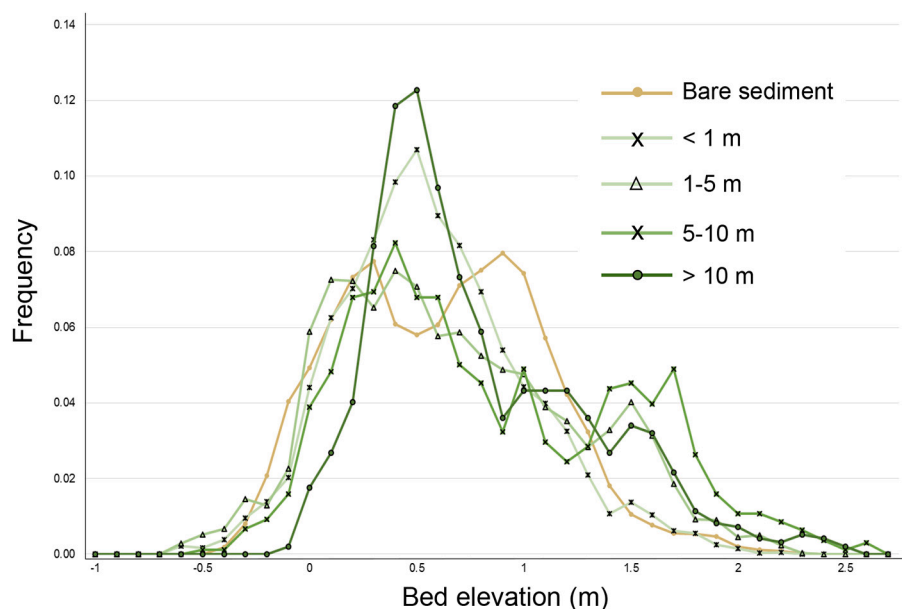


Fig. 10. Frequency distributions of river bed elevation (elevation above the lowermost point in the DEM; zero represents the mean water level) on alluvial bars of the Allier River, France, for bare soil surfaces and for surfaces under four riparian vegetation height classes. Adapted from Hortobágyi et al. (2017).

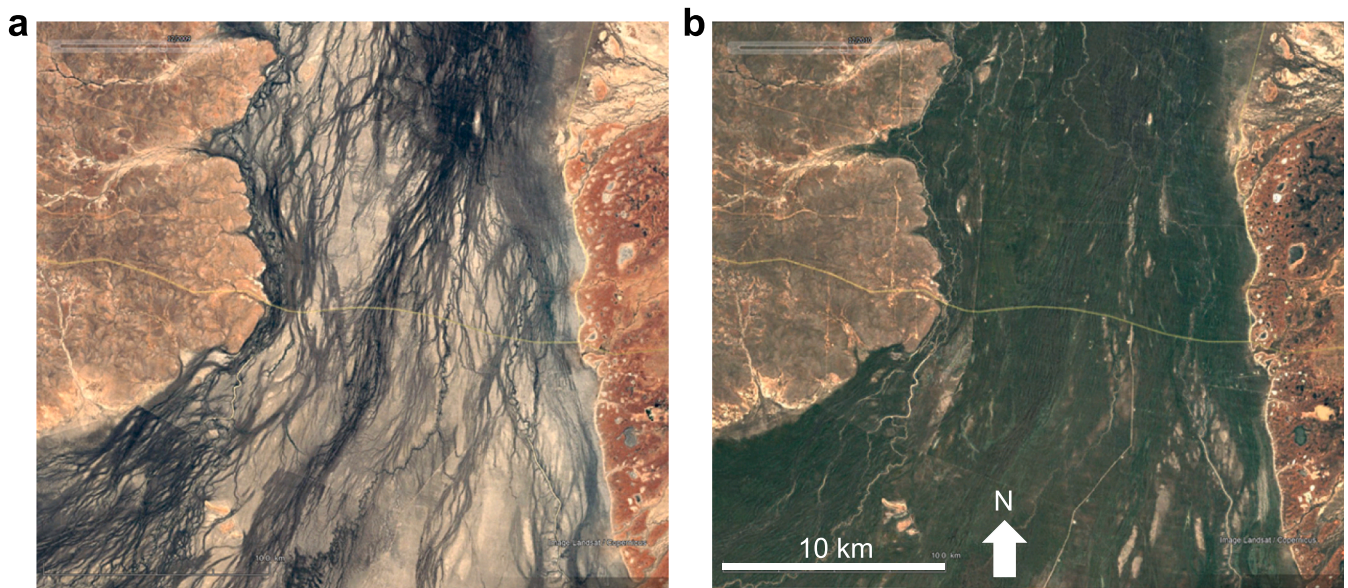


Fig. 11. Aerial photograph of the Cooper's Creek fluvial system near Durham, Central Australia, in a) 2009, and b) 2010. The year 2009 is very dry with less vegetation, while in 2010, the anastomosing channel-floodplain complex was much better vegetated. Aerial photograph taken from Google Earth™.

cases to very characteristic biosignatures in the riverscape at the reach scale. Braided styles occur but are not ubiquitous, and when present, they are frequently an expression of irregular hydrological regimes with flash floods, abundant bedload and erodible sandy banks (Mabbutt, 1977; Graf, 1988; Tooth, 2000; Conesa-García et al., 2022). In ephemeral river channels, vegetation can exert significant and, at times, dominant control over other physical factors. In particular, shrubs and

trees with deep and strong root systems that establish directly on channel beds in the periods between floods can favour localized sediment trapping and avulsion dynamics (Smith et al., 1997; Brookes et al., 2000). These effects increase riverscape complexity and can enhance the formation of very characteristic vegetated fluvial landforms within the active channel or active tract (*sensu* Gurnell and Petts, 2006: i.e., 'the area of essentially exposed bars and open water that indicates the zone



Fig. 12. Anabranching channels and pioneer vegetated ridges of various sizes in the active tract of the Marshall River, Australia (semi-arid biome). Aerial photograph taken from Google Earth™.

of frequent fluvial disturbance'). Such significant and quantifiable vegetation effects have been observed in sub-humid and semi-arid contexts in Australia, and commonly are associated with the formation of anabranching fluvial styles (Fig. 11; Nanson and Knighton, 1996; Gibling et al., 1998; Wende and Nanson, 1998; Tooth, 2000; Tooth and Nanson, 2000, 2004; Nakayama et al., 2002; Tooth et al., 2008; Erskine et al., 2009). Fielding et al. (1997) showed that in the sub-humid regions of northern Queensland, Australia, certain trees, notably *Melaleuca argentea* and *Pandanus* spp., can establish in the channel bed during dry seasons and survive floods and impact damages during wet season runoff events. These flood-tolerant species employ structural adaptations to survive, such as downstream-trailing habits, multiple stems, modified crowns, spongy bark and root regeneration. The observations by these authors indicated the occurrence of a powerful, positive biogeomorphological, scale-dependent feedback related to in-channel plant species modifying their environment by diverting flow, promoting sediment deposition, and creating locally favourable habitat conditions for seedling germination and plant growth. This research was the first to explicitly document in-channel bar development and fluvial style adjustment resulting from vegetation growth in a sub-tropical river with highly variable discharges (see also Fielding and Alexander, 1996).

Tooth and Nanson (2000) also described a similar positive biogeomorphological feedback in the riverscape of the semi-arid Marshall River, Australia. A pivotal role was shown to be played by tea trees (*Melaleuca* spp.), which initiated a positive feedback encompassing three stages. In the first stage, *Melaleuca* spp. colonization induces the formation and growth of sediment ridges of various dimensions (Fig. 12). The second stage involves interactions between growing ridges, with those in the lee of others being shielded from flood erosion, enhancing their survival chances. Ridge elongation occurs through the accumulation of trapped sediment after vegetation colonization on ridge tops. In the third final stage, elongated ridges merge with downstream ridges, creating long and stable landforms that divide the originally single channel into anabranches. Conversely, individual tea trees or small unprotected ridges are prone to erosion. Additionally, established vegetation and local large wood can determine the location of overbank flow in densely obstructed channels, leading to the scouring of floodplains or island surfaces (Wende and Nanson, 1998; Tooth and Nanson, 1999, 2000; Tooth et al., 2008). This process overall produces very characteristic biosignatures in the riverscape that can be attributed to vegetation effects without ambiguity (for a review, see Henriques et al., 2022).

The role of vegetation in sub-humid and semi-arid anabranching rivers extends from geomorphology to the associated distinct sedimentary facies (Fielding et al., 2009). Among the explanatory factors, Fielding et al. (2009) noted the critical role played by trees and other vegetation types morphologically, biomechanically and physiologically adapted to hydric stress and to occasional flash floods. These vegetation types colonize river channels, influence water and sediment flows, and result in characteristic sediment deposition patterns (see also Fielding et al., 2011).

5.4. Evidence of causality between vegetation and river morphodynamics from ancient alluvial records

Insights into the sufficiency of vegetation as a driver of river morphodynamics may also be gained from the geological sedimentary-stratigraphic record (SSR; Davies et al., 2020). The longevity of the SSR is such that it archives alluvium that both pre- and post-dates the evolution of vegetation. As a result, it provides the only tangible record of alluvium that was laid down by rivers where vegetation was unequivocally absent, i.e., prior to the Early Ordovician period (ca. 480 Ma) (Strother and Foster, 2021), as well as prior to other stepwise evolutionary innovations such as the Early Devonian appearance of roots (ca. 411 Ma) (Hetherington and Dolan, 2018) and of primary xylem ('wood') (ca. 407 Ma) (Strullu-Derrien et al., 2014), and the

Middle Devonian appearance of trees and forests (ca. 390 Ma) (Giesen and Berry, 2013; Stein et al., 2020; Davies et al., 2024). Thus, when studied in its entirety, the SSR provides a contrast between pre- and syn-vegetation alluvium that may enable shifts in the frequency distribution of particular sedimentary signatures (facies) to be identified and related to shifts in river morphodynamics (Davies et al., 2020).

Earlier surveys of published literature (e.g., Cotter, 1978; Davies and Gibling, 2010) reported a dramatic increase in the number of sedimentary rock successions interpreted as having been laid down in meandering rivers in strata post-dating the evolution of land plants. In the last decade, these surveys have spurred interest in: (i) the search for pre-vegetation meandering river deposits (e.g., McMahon et al., 2024); and (ii) questions regarding which vertical stratal signatures diagnose a meandering river planform (e.g., Santos and Owen, 2016; McMahon and Davies, 2018a). Consequently, the apparent trend of a sudden increase in facies interpreted as formed by river meanders during the Silurian and Devonian periods is no longer as pronounced. However, there remains a discernible shift in secular sedimentary facies characteristics, as evidenced at the outcrop scale, that differentiates pre- and syn-vegetation alluvium (and which historically resulted in the original split in numbers of interpreted meandering rivers). Among the features that demonstrably increase in frequency and abundance in the rock record are heterolithic lateral accretion sets (Davies and Gibling, 2010b; McMahon et al., 2022a), which signify the lateral migration of bank-attached bars typical of meandering rivers, as well as muddy floodplain associations (McMahon and Davies, 2018b) that are common in meandering rivers with reduced floodplain recycling. The relative rareness of such facies before the Silurian Period, as compared with their commonality following this interval, attests to a shift in either the creation or preservation of such features in stratigraphic synchrony with the evolution of land plants. Subsequent facies shifts are also apparent in the SSR, with sedimentary motifs attributable to island braided and anabranching configurations forming during the Middle Carboniferous Period (ca. 330 Ma), and interpreted as a consequence of physiological and biomechanical plant adaptations such as deeper rooting and woody debris (Davies and Gibling, 2010, 2011, 2013; Gibling and Davies, 2012; Gibling et al., 2014; Ielpi et al., 2014; Bennett et al., 2016).

The stratigraphic correlation between (i) a shift in the frequency distribution of sedimentary signatures that delineate different facies styles and (ii) the appearance of land plant fossils, does not prove causation. However, it does show that the trigger for the facies change must have been a unidirectional shift rather than a cyclic trigger such as tectonics or climate, which will have harmonized to similar conditions several times before and after the evolution of land plants, and so cannot be a sufficient explanation for the stratigraphic singularity (Davies et al., 2017, 2020).

Another facet of the ancient record supports the notion that the appearance of vegetation on a previously unvegetated planet was the trigger for the facies shift. The SSR archives information on a multitude of timescales, such that smaller outcrops of strata tend to focus onto small spatiotemporal sedimentary phenomena (Paola et al., 2018); thus, it is common to encounter phenomena whose formative timescales were analogous to the historicity recognizable in extant phenomena (Davies and Shillito, 2021; Davies et al., 2022b). From this perspective, the Silurian through to Carboniferous periods (ca. 440-300 Ma) yield strata that contain evidence for many small spatiotemporal scale biogeomorphological phenomena that were impossible to form before, and certainly are not known to be present before the evolution of land plants. Further, these phenomena may have been registered in the sedimentary record at various stages of their biogeomorphological development. Examples include mounds or scour hollows around standing vegetation (Rygel et al., 2004), log jam deposits (Gastaldo and Degges, 2007), or fluvial bars colonized by pioneer vegetation (Davies et al., 2021). Cumulatively, the first appearances of such biogeomorphological phenomena indicate that the maximum attainable phase of fluvial biogeomorphological succession (Corenblit et al., 2009b; see Section 3)

evolved in line with terrestrial flora.

Before land plants, by definition, all fluvial landforms existed in the geomorphological phase, but through the Ordovician and Silurian, it is plausible that small bryophytes and plants such as *Cooksonia* enabled the pioneer phase to be attained when the disturbance was subdued. Recent studies of Devonian systems have provided empirical evidence for the stepwise appearance of different phases of biogeomorphological succession. Early Devonian strata yield examples of bar tops colonized by *Zosterophyllum* as well as root structures in crevasse splays, both indicative of the pioneer phase (Davies et al., 2021). The earliest facies evidence for the biogeomorphological phase occurred within the Middle Devonian (ca. 390 Ma) strata, where standing plant fossils of cladoxyploid trees can be seen to have colonized channel margins and resisted flood events (Davies et al., 2024). In the Late Devonian, Frasnian-aged (ca. 375 Ma) strata yield the earliest empirical evidence for the achievement of the biogeomorphological phase, in the form of thin channel coals attesting to autogenic vegetation successions, and abundant large woody debris indicative of densely forested stands detached from high-frequency hydrodynamic disturbance (Davies et al., 2021). An even fuller suite of signatures is known from the end of the Devonian Period, where Famennian-aged (ca. 360 Ma) strata yield evidence for the oldest known log jams and chute channels that were colonized and stabilized by archaeopterid trees (Veenma et al., 2023).

Individual phenomena such as these can be recognized as the lowest orders within a spatiotemporal hierarchy of nested phenomena that scale up to the entire SSR (e.g., Ganti et al., 2020; Miall, 2022), in the same way that vegetation scales up from individual plants to entire biomes (Fielding and Alexander, 2001; Post, 2019; Larsen et al., 2021). Compelling evidence suggests that the accumulation of small-scale biogeomorphological interactions, enacted by even the tiniest ancestral land plants (e.g., Mitchell et al., 2023), revolutionized the ways in

which alluvial sediment accumulated, implying that there was also a concomitant change in fluvial behaviour. As such, the SSR confirms the significance of plant-river interactions at local scales, ranging from bedforms influenced by individual plants to the facies of landforms influenced by vegetational succession. It extends the notion of ‘scale-dependent feedback’ (see Gurnell et al., 2005; Francis et al., 2009; Corenblit et al., 2015) to its highest-order applicability (i.e., the ultimate evolutionary onset of vegetation) (Fig. 13). When combined with other evidence from experimental approaches and empirical observations of modern rivers, the ancient record confirms that vegetation is best considered to be an INUS condition (see Illari and Russo, 2014) for many fluvial phenomena of a defined spatiotemporal scale (Kleinmans et al., 2023). However, in many instances, the meandering style has a more direct causal relationship with other spatiotemporal scales of phenomena; for example, abundant mud weathered from the hinterland, or vegetated bar tops, which may themselves be contributory INUS factors to different order phenomena (such as meandering in this instance).

6. Perspectives in studying vegetation effects on river morphodynamics and a way forward

We have shown that many issues still need to be addressed to improve our understanding of the interactions between vegetation and river morphodynamics. Below, we outline some key issues that we suggest should be addressed alongside the development of a standardized trait-based approach for analysing vegetation responses to, and effects on, river morphodynamics. This trait-based approach will be presented in more detail in Part II.

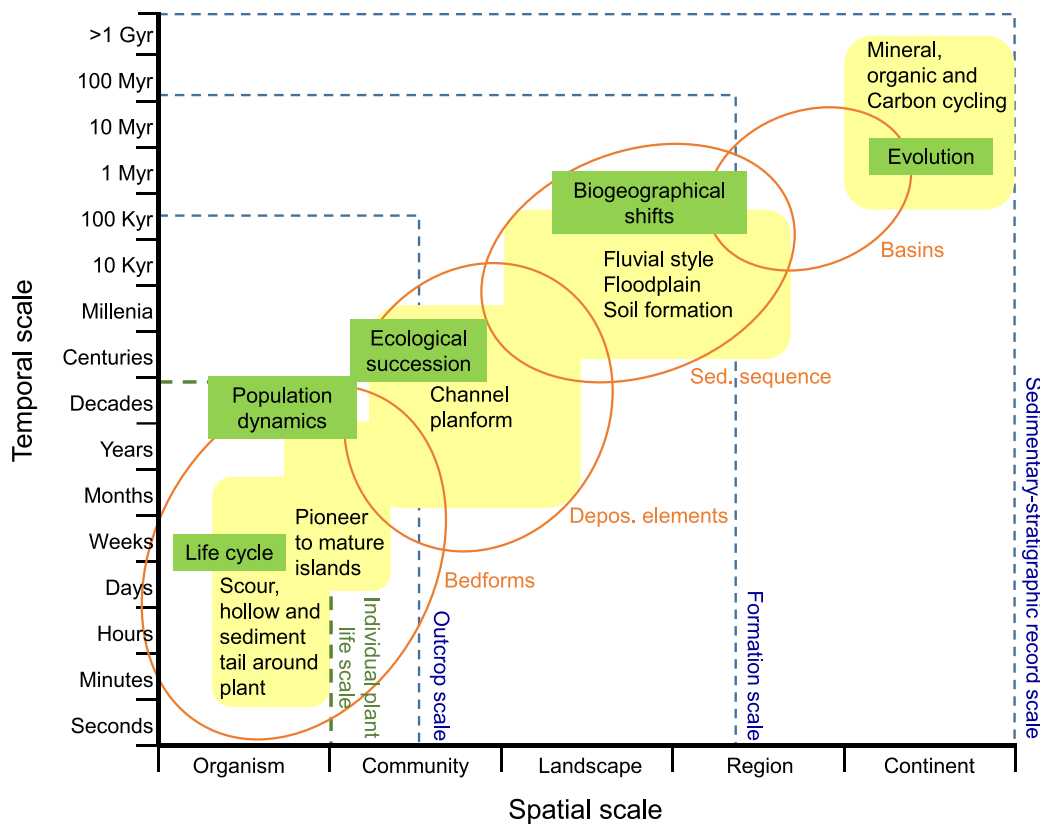


Fig. 13. Diagram showing examples of the relationship of approximate time and length scale in different phenomena, between which biogeomorphological feedbacks may exist. Green: vegetation; Orange: sedimentary phenomena; Yellow: Earth surface processes and landforms; Blue: expression within the sedimentary stratigraphic record. Depos.: deposition; Sed.: sedimentary. Modified after Davies et al. (2022b).

6.1. Combining mechanical and statistical approaches at the reach scale

Two research strategies must be combined to isolate plant effects from exclusive hydrogeomorphological river processes and adjustments above the local scale. First, the mechanistic approach based on flume experiments needs to be more intensively developed, particularly through improved ability to control hydrogeomorphological key drivers (e.g., sediment supply, grain size, channel geometry, energy slope, flood regime) and to select key vegetation characteristics with artificial or biological (e.g., alfalfa; [Tal and Paola, 2007](#)) material. This strategy will permit us to distinguish abiotic controls from vegetation treatments by formally assessing vegetation effects at the reach scale with sufficient control and replicability through robust experiments. To deliver this strategy, devices such as the *Metronome tidal facility* of Utrecht University (e.g., [Kleinhans et al., 2017](#)) should be developed. However, despite the advantages of this strategy, the upscaling of results to the real world would still remain challenging owing to the difficulty in reproducing morphological, biomechanical and life-history characteristics (traits) of vegetation. The complex properties of the riverscape emerge from an amalgam of individual plants, from short herbs to tall trees, and assemblages and patches with different, combined subsurface and aerial characteristics, which renders their simplification into a flume fallible. In other words, above the local spatial scale, by only using flume experiments, it will remain difficult to precisely determine the cause-and-effect relationships that link the hydrogeomorphic and vegetation drivers, and to characterize their reciprocal interactions that give rise to emergent and complex landscape behaviours.

The second complementary strategy consists of a standardized statistical approach whereby field observations about the vegetation effects on river morphodynamics are collected from different reaches to better control the variability in geomorphological responses related to the physical confounding factors. These observations could then be used to test differences in geomorphological outcomes with and without vegetation effects within a classical experimental framework (e.g., before-after or control-impact, and ideally both) ([Christie et al., 2020](#)). The main challenges of this strategy are: (i) the scarcity of suitable reaches and river systems for collecting a robust dataset, as well as the inherent variability in field conditions that introduces noise and can weaken the reliability of replicated measurements; and (ii) the lack of a standardized protocol for quantifying vegetation structures in a manner that would establish a relationship with river morphodynamics in terms of vegetation responses and effects (see Part II).

6.2. Linking geomorphological changes under vegetation control across spatiotemporal scales

We need to be cautious when attempting to generalize small-scale data to data at larger spatial and temporal scales, even when using the most robust observations obtained at local scales. The patterns and processes that we observe locally (e.g., the formation of sediment tails downstream of individual plants) may not be the ones that explain river landscape organization at larger scales. Furthermore, in order to quantitatively and robustly determine where and to what extent riparian vegetation (from herbs to mature trees) controls river morphodynamics at a reach scale, data from a wide set of climatic, hydrogeomorphological, anthropogenic and biological situations (see [Table 1-4](#)) are required. The exploration of large databases (standardized if possible) may offer the possibility to define the range and characteristics of vegetation responses and effects within a multidimensional statistical domain. Within this statistical domain, functional groups of plant responses to, and effects on, river morphodynamics must be defined based on standardized databases of vegetation traits (see Part II). It is also important to analyse more critically what upscaling and downscaling mean, both conceptually and methodologically. For example, it might be expected that the greater the number of hydrogeomorphological variables that are affected across spatiotemporal scales by vegetation, the

more significant will be the overall effect of vegetation on river morphodynamics (considering the measurement of plant traits at the individual, population and community levels). Again, however, this expectation remains to be tested.

As previously proposed by [Dietrich and Perron \(2006\)](#) and [Corenblit et al. \(2011\)](#), we assert that singular (unique) biotic signatures of vegetation in fluvial geomorphology may not exist at any of the observed spatiotemporal scales. Instead, it may be the frequency of distributions of individual or combined geomorphological parameters associated with channel dimension, sediment texture and facies organization, and the riverscape at different scales, that are modulated by vegetation. Variations in the frequency distributions of these parameters should be correlated with certain vegetation traits, or combination of traits, and may serve as a robust method to discern vegetation effects. Frequency distributions of key parameters that are embedded in a hierarchy of spatial scales are potentially discernible with statistical approaches, and this should be explored. The ideal situation would be to isolate field situations where it is possible to add abiotic controls to the biotic observations. This would furnish a basis for comparing 'biotic' and 'abiotic' frequency histograms and gaining a deeper understanding of how, and to what extent, vegetation modulates fluvial landforms and landscape components over the various spatiotemporal scales.

6.3. Using new technologies more extensively

Observational datasets of topography, sediment texture, and vegetation morphological and physiological traits are needed at higher frequencies, spatial coverages, and resolutions to enhance process-based understanding across all spatial scales, preferably utilizing low-cost sensors directly implanted in the field.

Time-lapse cameras and video recording could be widely used to better capture and understand local scale processes in 2D and 3D in the field, such as pioneer island accretion or bank retreat related to vegetation effects. Remote sensing technology could be used to better quantify and understand local controls on vegetation recruitment and growth, by combining information captured by near infra-red, red-edge, thermal sensors, LiDAR and photogrammetric technology. Improved observation capacity using remote sensing should also underpin multi-temporal surveys to better understand the optimal spatiotemporal windows for plants to establish and affect river morphodynamics ([Huylenbroeck et al., 2020](#)). OSL (Optically Stimulated Luminescence) or other geochronological methods should be more widely used to document channel-vegetation interaction over longer timescales (decades, centuries and millennia) (e.g. [Tooth et al., 2008](#)). Machine learning methods, especially deep learning methods, become increasingly able to combine such rich datasets ([Stupariu et al., 2022](#)) and thus could be relevant to discovering patterns of vegetation effects on river hydrogeomorphology at local, reach, and riverine landscape scales.

6.4. Using global databases to assess how global environmental change will influence interactions between vegetation and river morphodynamics

Global environmental change models project significant modifications in regional temperatures and precipitation patterns, as well as changes in land cover. These modifications will ultimately affect peak flows, sediment delivery, and biological conditions, influencing vegetation recruitment, establishment, growth, and succession (e.g., [Schneider et al., 2013](#); [Pumo et al., 2016](#)). This is likely to change the relationship between remobilization forces related to the flood regime and resistance forces associated with the relation between substrate properties and vegetation traits across riverscapes worldwide. Future biogeomorphological successional trajectories need to be monitored with high accuracy alongside environmental variables in various bioclimatic contexts subjected to significant changes in hydroclimatic regime. At a global scale, existing databases (e.g., hydrological series, aerial and Landsat or Sentinel archives, Google Earth Engine resources,

lists of groups of plants) should be more deeply and extensively explored, generating standardized frameworks for understanding the effect of changes in seasonality on plant recruitment, establishment, growth and successional patterns along fluvial corridors. This effort is necessary to enhance projections of how vegetation will respond to, and affect, river morphodynamics worldwide in the near future. This effort also will facilitate the development and validation of reliable numerical models of river landscape changes based on plant traits. Such models would offer an opportunity to formally establish connections between plants and river morphodynamics (see Part II).

6.5. Improving understanding of ancient rivers operating at different stages of plant evolution

As the ancient rock record provides a window into alluvium deposited at various stages during the evolution of plant life, case studies of the interactions between fluvial products and fossil plants permit insights into the various impacts that the arrival of plants had on fluvial sedimentation. The present tendency to proclaim increasingly older sedimentary facies as the products of pre-vegetation meandering rivers (e.g., Ganti et al., 2019; Valenza et al., 2023) is arguably questionable because: (i) such claims are commonly equivocal owing to a reliance on speculative models using estimate-heavy quantitative calculations that frequently contradict empirical evidence (Kleinhans et al., 2023; McMahon et al., 2024); and (ii) the ultimate inference from these claims, that vegetation is an INUS condition for meandering, is already known (Kleinhans et al., 2023). Conjecturing modelled calculations to have primacy over geological evidence may yield confusion as to what information can be gained from direct observations of ancient strata. Direct observations should not be underestimated as a research tool, as it is clear from case studies of Devonian and younger strata that novel plant-sediment interactions can be identified in the rock record (Rygel et al., 2004; Allen and Gastaldo, 2006; Gastaldo and Degges, 2007; Hillier and Williams, 2007; Gibling et al., 2010; Bourquin et al., 2011; Neff et al., 2011; Rößler et al., 2012; Allen et al., 2014; Davies et al., 2021, 2022a, 2024; Trümper et al., 2020, 2022; McMahon et al., 2022b; Mottin et al., 2022; Gastaldo et al., 2023; Veenma et al., 2023). Increasing the number of such studies will permit a more refined history of the impact of land plants as biogeomorphological agents, extending our perspective of empirical evidence for their role beyond the finite historical records that impede our understanding of extant biogeomorphological systems (Larsen et al., 2021). Fluvial strata dating to the earliest land plant communities in the Ordovician and Silurian periods are at present particularly overlooked.

7. Concluding remarks

This article lays a preliminary theoretical foundation for the development of a new trait-based functional approach for understanding the interaction between various types of plants and alluvial rivers. In particular, the floristic (taxonomic) approach generally used is limited when exploring vegetation effects on river morphodynamics. The role of biological variability and diversity needs to be explored much more deeply using an approach based on the statistical description of the functional linkages between the life history, morphological and biomechanical characteristics of plants, and the geomorphological characteristics of rivers. This theme is explored in depth in Part II of our review.

Author contributions

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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