Fluvial biogeomorphological feedbacks from plant traits to the landscape: lessons from French rivers in line with A.M. Gurnell's influential contribution

Dov Corenblit[1] and Johannes Steiger[2]

[1]Laboratoire ecologie fonctionnelle et environnement
[2]Universite Clermont Auvergne

November 20, 2023

Abstract

Research in fluvial biogeomorphology largely aims to promote our understanding of the interactions between riparian vegetation and fluvial morphodynamics within riverine ecosystems. Starting at the end of last century, Angela M. Gurnell has made a major contribution to fluvial geomorphology by considering, in addition to water flow and sediment transport, explicitly riparian, and later also aquatic vegetation and thus significantly promoted the fluvial biogeomorphological approach from its beginnings until today. The objective of the present paper is to present a set of studies and results obtained over the last twenty years by the authors and many collaborators, including Angela M. Gurnell, on a panel of French rivers: Tech, Garonne, Isère and Allier Rivers. In particular, feedback mechanisms between fluvial morphodynamics and riparian vegetation dynamics were investigated directly in the field and also using high resolution remote sensing at the scale of individual plants, populations, communities and landscapes, as well as during semi-controlled *ex situ* experiments at the scale of individual plants. Collectively, the authors' research conducted over the past 20 years contributed to elucidate some key aspects of the feedback dynamics between the lowest and highest levels of the riparian ecosystem organisation. This article presents and discusses those key aspects. The gradually obtained results contributed to better understand and quantify feedbacks between river morphodynamics and vegetation at nested spatiotemporal scales, from plant species traits to the riverine landscape. Furthermore, the biogeomorphological approach advocated for more than twenty years now, has clearly helped to contribute to the enlargement of the discipline of geomorphology to ecology as well as evolutionary ecology, and to the development of a more integrative vision to study earth surface processes.

Fluvial biogeomorphological feedbacks from plant traits to the landscape: lessons from French rivers in line with A.M. Gurnell's influential contribution

Running title: Biogeomorphological feedbacks from plant traits to the landscape

Dov Corenblit[a,b*], Johannes Steiger[b]

[a]Université de Toulouse, CNRS, Laboratoire Écologie Fonctionnelle et Environnement, 31062 Toulouse, France.

[b]Université Clermont Auvergne, CNRS, GEOLAB, 63000 Clermont-Ferrand, France.

***Corresponding author:** Dov Corenblit: jean-francois.corenblit@univ-tlse3.fr

Acknowledgments

The authors first warmly thank Angela M. Gurnell for her invitation to contribute to this special issue and second are very grateful for the long and very rewarding collaboration which started 25 years ago at the University of Birmingham and largely contributed to determine our professional trajectories. We also thank all co-authors from our papers we have cited in this contribution for the successful achievement of the presented biogeomorphological investigations. The authors acknowledge the French National Research Agency (ANR) that supports the Project-ANR-21-CE32-000 "NUMRIP".

Abstract

Research in fluvial biogeomorphology largely aims to promote our understanding of the interactions between riparian vegetation and fluvial morphodynamics within riverine ecosystems. Starting at the end of last century, Angela M. Gurnell has made a major contribution to fluvial geomorphology by considering, in addition to water flow and sediment transport, explicitly riparian, and later also aquatic vegetation and thus significantly promoted the fluvial biogeomorphological approach from its beginnings until today. The objective of the present paper is to present a set of studies and results obtained over the last twenty years by the authors and many collaborators, including Angela M. Gurnell, on a panel of French rivers: Tech, Garonne, Isere and Allier Rivers. In particular, feedback mechanisms between fluvial morphodynamics and riparian vegetation dynamics were investigated directly in the field and also using high resolution remote sensing at the scale of individual plants, populations, communities and landscapes, as well as during semi-controlled *ex situ* experiments at the scale of individual plants. Collectively, the authors' research conducted over the past 20 years contributed to elucidate some key aspects of the feedback dynamics between the lowest and highest levels of the riparian ecosystem organisation. This article presents and discusses those key aspects. The gradually obtained results contributed to better understand and quantify feedbacks between river morphodynamics and vegetation at nested spatiotemporal scales, from plant species traits to the riverine landscape. Furthermore, the biogeomorphological approach advocated for more than twenty years now, has clearly helped to contribute to the enlargement of the discipline of geomorphology to ecology as well as evolutionary ecology, and to the development of a more integrative vision to study earth surface processes.

Keywords: Fluvial biogeomorphology, biogeomorphological feedback, riparian vegetation, *Populus nigra* , black poplar, ecosystem engineer, plant traits.

Introduction

In order to fully understand river behaviour and trajectories of change, Angela M. Gurnell early pointed out the need to study interactions between the biological and physical compartments of ecosystems, i.e., the responses of organisms to the physical environment and their effects on that physical environment (Gurnell and Gregory, 1984, 1995; Gurnell, 1995). Research in fluvial biogeomorphology largely aims to promote our understanding of the interactions between riparian vegetation and fluvial morphodynamics within riparian ecosystems. Angela M. Gurnell has made a major contribution by considering explicitly vegetation, first riparian (living vegetation, propagules and large woods) and then aquatic, in addition to water flow and sediment transport into fluvial geomorphology and thus to promote the fluvial biogeomorphological approach from the end of the last century until today (e.g., far from exhaustive: Gurnell, 1997; Gurnell et al., 2000, 2001, 2004, 2005, 2006, 2012, 2013, 2016a, 2016b, 2018, 2019; Gurnell and Petts, 2002, 2006; Gurnell, 2014; Gurnell and Grabowski, 2016; Gurnell and Bertoldi, 2020; Gurnell and Bertoldi, 2022). A bibliographic research on the Web of Science (all databases) using the combined terms "riparian vegetation" + "geomorphology" + "river*" showed that out of a total number of 711 articles archived on 11$^{\text{th}}$ November 2023, more than 12% were authored or co-authored by A.M. Gurnell, which represents 86 articles. The second-best score is 33 articles (Fig. 1).

The biogeomorphological approach applied to rivers is necessarily ambitious because requires skills in geomorphology and plant ecology and because the modalities of interactions between hydrogeomorphological components and riparian vegetation are multiple and nested at various spatiotemporal scales. Thanks to Angela M. Gurnell's influential research and contribution to fundamental and applied river sciences, fluvial biogeomorphology is now well situated at the interface between, geomorphology, ecology and river management (e.g., Gurnell et al. 2016a,b).

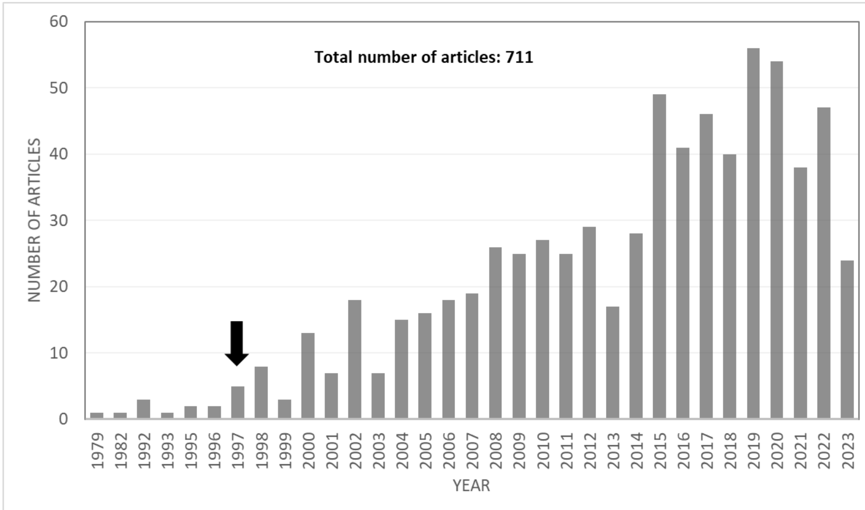

Figure 1. Number of peer reviewed journal articles per year using the combined terms "riparian vegetation" + "geomorphology" + "river*", as archived on Clarivate Web of Knowledge (all databases) (https://www-webofscience-com.inee.bib.cnrs.fr/). A.M. Gurnell's first article using these terms was published in 1997 (see vertical black arrow) and her name comes out first with more than 12% of all articles authored or co-authored. Accessed on 11th November 2023.

The objective of this article is to present a set of studies and results from the past 20 years obtained by the authors and many collaborators, including Angela M. Gurnell, on a panel of French rivers: Tech, Garonne, Isère and Allier Rivers. In particular, *feedbackmechanisms* between fluvial morphodynamics and riparian vegetation dynamics were investigated directly in the field and used high resolution remote sensing at the scale of individual plants, populations, communities and landscapes as well as during semi-controlled *ex situ* experiments at the scale of individual plants. Collectively, the authors' research contributed to elucidate some key aspects of feedback dynamics between the lowest and highest levels of the riparian ecosystem organisation. This article presents and discusses those key aspects.

Feedbacks between vegetation and fluvial geomorphology at nested spatiotemporal scales

Riparian ecosystems are among the most dynamic and variable environments on Earth's surface in terms of structure and function, making them a target of many ecological restoration projects (Amoros and Petts, 1993; Naiman and Décamps, 1997; Muñoz-Mas et al., 2017; Gonzalez et al., 2018; González, et al. 2022; O'Briain et al., 2023). They represent land-water interface zones where matter and energy are concentrated, transit, are stored, and transformed. The flows of water, sediment, organic matter – from dissolved organic matter to large woods –, and seeds that pass through, both cyclically (hydrological regime) and stochastically (floods), contribute to maintain a high degree of heterogeneity in the mosaic of habitats (Townsend, 1989; Gurnell et al., 2005). This spatiotemporal heterogeneity generates strong ecological gradients and sometimes exceptional levels of biodiversity, including a variety of survival and reproduction strategies in a shifting mosaic (Ward, 1989; Schnitzler et al., 1992; Ward et al., 2002; Stanford et al., 2005; Bornette et al., 2008).

Hydroecological theoretical models are based on the postulate that the structure and functioning of aquatic and riparian communities can be explained by considering the links between life history traits of species and the geomorphological structures and processes that govern flows of matter and energy (Vannote et al., 1980; Newbold et al., 1982; Pickett and White, 1985; Amoros et al., 1987; Junk et al., 1989; Townsend, 1989; Ward, 1989; Tockner et al., 2000). Models such as the River continuum concept, Flood pulse and Flow pulse, Nutrient spiralling, Patch dynamics, were nevertheless developed according to a type of Physical habitat template approach (*sensu* Southwood, 1977), that is, focusing strictly on the *a priori* unidirectional effect of the physicochemical heterogeneity on biodiversity and ecosystem functioning. Previous research on riparian ecosystems has not sufficiently considered how and to what extent the three spatial dimensions of riverine ecosystems are controlled by riparian vegetation.

Certain plant species and assemblages have a profound and lasting impact on the structure and function of riparian ecosystems by modulating matter and energy fluxes and modifying substrate cohesion (Gurnell et al., 2012). Riparian plant species (e.g., the black poplar *Populus nigra* L. in the Northern hemisphere) that significantly affect hydrogeomorphological processes and fluvial landforms have been identified as ecosystem engineers (*sensu* Jones et al., 1994), keystone species (*sensu* Paine, 1966), and, more recently, as potential niche constructors *sensu* Odling-Smee et al. (2003) (Edwards et al., 1999; Gurnell and Petts, 2006; Corenblit et al., 2009b; Francis et al., 2009).

How, and to what extent, the structure and function of riparian ecosystems are controlled by abiotic-biotic feedbacks across various spatiotemporal scales has become an important issue in fluvial biogeomorphology. This question must be addressed from the fine scale of the individual plant, the microhabitat and single hydrological event to the coarse scale of plant community mosaic, the fluvial corridor and the hydrosedimentary regime. In particular, the mechanisms by which engineer plants respond to, and shape, the mosaic of riparian habitats are not fully understood. Some evolutionary adaptations of plants in response to the hydrogeomorphological disturbance regime such as floating seeds, synchronization of reproduction with the flood regime (Junk et al., 1986; Guilloy-Froget et al., 2002), vegetative reproduction in addition to sexual reproduction strategies (Barsoum, 2002; Francis and Gurnell, 2006; Moggridge and Gurnell, 2009), and biomechanical stem flexibility in order to avoid uprooting during flood events (Karrenberg et al., 2002; Lytle and Poff, 2004; Bornette et al., 2008), help riparian plants to survive despite high physical constraints. These adaptations, combined with phenotypic plasticity, allow engineer plants to mechanically resist to drag force in the flow and to influence their riverine environment. By trapping sediments, organic matter, and seeds, engineer plants can create, build, and maintain riparian habitats that are beneficial to other plant species, including other engineer plants.

In addition to the role of vegetation assemblages (i.e., community scale) in shaping the hydrogeomorphic features of riverine ecosystems, specific life history, morphological and biomechanical traits related to distinct engineer species also play an important role. In the absence of large, destructive floods, the short-range actions of plants – within their own stands and immediately downstream – typically result under adequate conditions in the accumulation of fine sediment, nutrients, organic matter, which improve habitat quality. In addition, with the deposition of seeds (e.g., Goodson et al., 2001, 2002; Gurnell et al., 2004, 2006; Corenblit et al., 2009a, 2016a), the improved habitat quality, in turn, promotes the establishment and growth of new plant species, including other engineer species. This process can increase the likelihood of pioneer woody engineer species such as *P. nigra*reaching sexual maturity (Corenblit et al., 2014a, 2018).

The synchronized process of fluvial landform construction and plant establishment/growth/succession can lead to the emergence of characteristic biogeomorphological landforms such as fluvial islands that are the result of engineering effects of riparian plants (Gurnell et al., 2001). These positive abiotic-biotic feedback dynamics which potentially affect the fluvial style (e.g., island braided rivers*sensu* Gurnell et al. 2019) are consistent with the action of ecosystem engineers (*sensu* Jones et al., 1994; Gurnell and Petts, 2006) and, potentially, niche constructors (*sensu* Odling-Smee et al., 2003; Corenblit et al., 2015). In turn, the effects of riparian engineer plants on the hydrogeomorphological components of riverine ecosystems involve a set of responses in these plants, from the individual to the community mosaic level and vice versa. This abiotic-biotic feedback is organized in three stages (Fig. 2):

(1) Initial response of plants to hydrogeomorphological constraints: at the beginning of growth and succession, plants must respond to a variety of hydrogeomorphological constraints, including mechanical forces (e.g., stream flow, erosion and sediment burial) and physiological stress factors (e.g., prolonged immersion and drought). These constraints act as a powerful filter for the colonisation, establishment and growth of engineer plants in exposed areas on alluvial bars. However, they can also stimulate morphological and biomechanical responses that increase plant resistance to these constraints.

(2) Effects of engineer plants on hydrogeomorphological components: the mechanical resistance allows plants to act passively on their hydrosedimentary and geomorphological environment. Once established, engineer plants can modify the hydrogeomorphological components of their environment in a variety of ways. For example, their roots can increase substrate cohesion, which can help to stabilize bars and banks and prevent erosion. Their trunks, branches and leaves can promote trapping of sediment and organic matter, which can help to build up islands, floodplains and create new habitats.

(3) Plant response to changes in the hydrogeomorphological environment: as engineer plants modify their environment, they can create positive feedback loops that further enhance their impact and growth (Corenblit et al., 2009a, 2014, 2018) as well as negative feedback loops translated into the transition toward stabilized and mature stages of the vegetation succession on raised alluvial surfaces (Bendix and Hupp, 2000; Corenblit et al., 2007; Corenblit et al., 2009a). For example, the increased stability of river bars and banks and their vertical accretion provided by engineer plants can reduce erosion and sediment burial, which can create more favourable conditions for the establishment of other competitive plants. This can lead to the development of complex and diverse riverine ecosystems with increased beta diversity at the landscape scale (Gurnell et al., 2005).

Hosted file

`image2.emf` available at https://authorea.com/users/701832/articles/688065-fluvial-biogeomorphological-feedbacks-from-plant-traits-to-the-landscape-lessons-from-french-rivers-in-line-with-a-m-gurnell-s-influential-contribution

Figure 2: Multi-scale theoretical model of the feedback between riparian vegetation dynamics and river morphodynamics.

Individual plant and population level feedbacks: response and effect traits of *Populus nigra*

In settings exposed to high tractive forces and sediment erosion or burial during floods, high temperatures and hydric stress during summer low flows, such as on alluvial bars, the completion of the life cycle of certain woody pioneer riparian species such as *P. nigra* requires a progressive modification of hydrogeomorphological conditions and habitat, from germination to sexual maturity. The latter is reached when the habitat and its topographic surface attain higher, more stable levels, characterized by the deposition and accumulation of finer sediments, nutrients, and organic matter, and less exposed to the risk of destruction by floods.

Individual plants may form together at the colonization stage more or less compact and monospecific woody populations which are very relevant for the study of biogeomorphological feedback from the individual to population levels. In riparian contexts in the European Northern hemisphere, *P. nigra* has become a model species for field studies but also *ex situ* experiments (Figs. 3 and 4).

3.1. Responses of aerial and underground parts of riparian plants to hydrogeomorphological *in situ* constraints

When individuals of *P. nigra* establish on alluvial bars in dynamic rivers, they can strongly affect fluvial geomorphology by trapping fine sediments on alluvial bars during floods, and thus build new biogeomorphological landforms (Gurnell, 2014; Hortobágyi et al., 2018a). The engineer effect of *P. nigra* on alluvial bars depends on its architecture, biomass, and exposure to mechanical stress. The species has a strong phenotypic plasticity that allows to adjust its physiological, morphological and biomechanical traits according to local hydrogeomorphological conditions. The quantification of the morphological and biomechanical variation of response traits within*P. nigra* populations which depend on exposure to mechanical constraints related to flow is essential to better understand why, to what extent, and where the black poplar is able to modulate geomorphology and thus gain in its survival, growth, and reproduction.

In an empirical study conducted on the Allier River, Hortobágyi et al. (2017) quantified the variation in response traits of *P. nigra*within a population that was two years old, based on three levels of exposure to mechanical constraints. In highly exposed areas, at the head of an alluvial bar, saplings developed response traits that allow for greater resistance, including a reduced size (avoidance strategy; see Bornette and Puijalon, 2011; Puijalon et al., 2011), a flexible and inclined stem, and also a more robust root system (tolerance strategy; see Bornette and Puijalon, 2011; Puijalon et al., 2011). In a highly exposed context, avoidance morphological and biomechanical responses led to a decrease in drag during floods. These responses that increase the resistance of young individuals nevertheless limit the engineer effect, i.e., their ability to trap fine sediment and nutrients in relation with increased surface biomass and roughness. This limitation of the engineer effect of black poplar in the most exposed areas, at the head of the bar, is therefore translated by a limitation of sediment trapping and niche construction at the very early stage of establishment.

This observation suggests the existence of a functional compromise in the expression of traits between resistance to floods (i.e., improvement of survival) and niche construction (i.e., improvement of habitat conditions under biotic control and therefore improvement of resource acquisition and growth). In less exposed areas of alluvial bars – in the middle part and downstream of the bars as well as within near secondary channels – young poplars developed a wider, longer, less flexible, and less inclined stem, as well as larger leaves. This expresses a prioritization of resource acquisition and competition abilities and at the same time the possibility for niche construction during ordinary floods. The total length (underground part + aerial part) of the plants is maximal at the tail of the bar with a notable effect on the trapping of fine sediments.

Complementary observations of individual roots system on the same alluvial bars showed that plant burial by fine sediment systematically stimulates the production of adventitious roots and aerial biomass, which in turn increases sediment trapping (Ding, 2014). This was interpreted as a positive biogeomorphological feedback of sedimentary accretion and plant growth. The construction of fluvial landforms by black poplar cohorts seems to correspond to a positive niche construction strategy leading to the progressive reduction of mechanical constraints and to a modification of the habitat that positively influences the survival, growth, and ultimately the sexual reproduction of poplars (Corenblit et al., 2016b, 2018, 2020a,b). Biogeomorphological processes occurring at a small scale caused by different morphological and biomechanical plant traits therefore may have an influence on the processes of fluvial landform construction at a larger spatial scale (Merritt, 2013; Corenblit et al., 2015; O'Hare et al., 2016; Diehl et al., 2017).

3.2. Responses of the aerial and underground parts to hydrogeomorphological constraints in experimental *ex situ*conditions

As observed in the field, specific morphological and biomechanical response traits of avoidance and tolerance (resistance traits) allow*P. nigra* to effectively colonize alluvial bars and thus to modulate hydrogeomorphological processes (Fig. 3). Quantitative experimental studies of the modulation of riparian plant morphology and biomechanics induced by hydrogeomorphological constraints permit to better understand under semi-controlled conditions how plants can colonize a physically highly exposed and naturally disturbed fluvial landform. These modulations of individual plants potentially translate the development of a resistance or avoidance strategy, or both, in these plants, which ultimately can induce changes in fluvial morphodynamics at the landscape scale.

Experimental research should particularly provide a quantitative answer to two key questions such as: How does drag force caused by stream flow affect the growth of *P. nigra* ? How do successive sediment burials and the accumulation of sediment influence the growth of*P. nigra* ? The response of *P. nigra* to these two categories of mechanical constraint determines both the efficiency of the growth of individuals to sexual maturity and the evolution of fluvial landforms. Garófano-Gómez et al. (2018) conducted an *ex situ* experiment in semi-controlled conditions at the GEOLAB laboratory in Clermont-Ferrand, France, to dissociate the effects of hydrogeomorphological factors acting on anchorage and plant growth. The experiments targeted the morphological and biomechanical responses of young *P. nigra*individuals. One hundred and twenty-eight *P. nigra* cuttings of Jean Pourtet variety were planted in one hundred and twenty-eight flexible bags of 0.6 m^3 filled with Allier River sand with an automatic irrigation system adapted to a filtering substrate. This system included a microporous ring for automatic irrigation for each bag. The young *P. nigra* individuals were subjected to two types of constraints during a full growing season (from March to November), i.e., three treatments in total: (1) no constraint (this population without any treatment served as a control); (2)

sediment burial with a calibrated grain texture; (3) mechanical constraint reproducing a calibrated hydraulic constraint repeated at a certain frequency and intensity; (4) the two constraints combined on a population of cuttings.

The growth of the aerial and root parts was precisely quantified by measuring numerous morphological and biomechanical traits of the underground and aerial parts: morphological and architectural soft traits (e.g., maximum height, cumulative length of stems, growth rate, stem diameter, root branching rate, root depth, ratio of elongation and biomass between the aerial and underground parts, number of structural roots, ratio of biomass between fine roots and structural roots, root growth orientation, specific leaf area); anatomical and biomechanical traits (flexural stiffness, stem breakage resistance, and cell size). Hard traits were also measured at the end of the experiment, including resistance to pulling out with a winch test. The measurement of morphological and architectural parameters of the aerial part was carried out continuously on the experimental site during growth. The measurements of the root part were performed in the laboratory at the end of the growing season. 2D and 3D modelling techniques, including multi-image photogrammetry, were used to automatically reconstruct and measure plant architecture.

Results indicated a significant effect of the treatments on the size, position, and type of roots. Sediment burial (SB) induced the production of numerous fine adventitious roots, and the application of stem bending (DF) induced the production of more solid basal structural roots. Morphological responses were more pronounced in the sediment burial treatment than in the stem bending treatment. The control (C) showed reduced aerial biomass compared to the treatments, but a root-to-shoot biomass ratio in favour of the roots. The combination of bending and sediment burial (DFSB) produced a positive surface growth response. DF showed a significantly higher biomass of basal roots than SB and DFSB, while SB had a higher biomass of lateral roots.

These findings are consistent and complementary with the *in situ*observations (Ding, 2014; Hortobágyi et al., 2017; Corenblit et al., 2020b). They provide evidence of the high morphological and biomechanical plasticity of the black poplar, which ensures its establishment in various conditions of exposure to shear stress and sediment burial and thus its capacity in high density to collectively affect sediment transport.

Hosted file

`image3.emf` available at https://authorea.com/users/701832/articles/688065-fluvial-biogeomorphological-feedbacks-from-plant-traits-to-the-landscape-lessons-from-french-rivers-in-line-with-a-m-gurnell-s-influential-contribution

Figure 3: Observed feedback at the individual level. (a) PopTrait *ex situ* experiment in Clermont-Ferrand for understanding*P. nigra* responses to biomechanical constraints; (b) sediment tail downstream of a multi-stemmed black poplar on an alluvial bar of the Tech River. The morphology of the sediment tail is correlated with morphological traits of the black poplar individual. Photographs: Virginia Garófano-Gómez (a) and Aurélien Chabanon (b).

3.3. Effect of *Populus nigra* at the scale of the alluvial bar

Corenblit et al. (2016b) established on alluvial bars of the Garonne River: (i) the modality of variation of annual sedimentation and topographic aggradation rates within *P. nigra* cohorts of different ages, and (ii) the physiological response (growth rate, production of adventitious roots, suckers, and surface stem density) associated with hydrogeomorphological modifications under*P. nigra* control. Within the strongly channelized river section of the Garonne River downstream of Toulouse studied (Steiger et al., 2000, 2001), populations of black poplars establish on alluvial bars and predominantly modulate the dynamics of fine sediments and fluvial landforms. Following the cessation of massive gravel extraction in the main channel during the 1980s, successive dense cohorts of*P. nigra* have successfully colonized the entire alluvial bars since mid of the 1990s. These very dense cohorts, which settle from upstream to downstream on point bars in successive meander loops, induce very important sedimentary accretion and landform stabilization.

Over a period of thirty years, the geomorphological characteristics of wooded alluvial bars have evolved in close relationship with the dynamics of cohort establishment and plant growth. The geomorphological characteristics of these bars (topography, thickness, and texture of sediments) are statistically linked to the spatial distribution and intensity of establishment by the successive cohorts of *P. nigra* . In return, geomorphological changes strongly influence the physiognomy of cohorts (density, diameter, size, and architecture of individuals) as well as the floristic structure of the herbaceous layer, with the transition from open units with high plant biodiversity of opportunistic annual and biannual species to closed units under mature black poplar cover dominated in the understory strata by *Rubus* , *Urtica* ,*Convovulus* , and *Galium* spp. This reciprocal causal relationship between geomorphological dynamics and plant dynamics is suggested by a strong correlation between key geomorphological and ecological variables measured *in situ* and from aerial photographs taken by the IGN between 2000 and 2010 (Corenblit et al., 2016b). In addition, this study found that recruitment and establishment dynamics of *P. nigra* are controlled by the engineer effects of this species through a facilitation effect linked to the obstacle and protection effect offered to new seedlings and saplings by upstream cohorts.

The construction of the biogeomorphological units "wooded point bars" is the result of a positive biogeomorphological feedback of stabilization and closure of the environment linked to the massive trapping of sand by dense *P. nigra* cohorts and the vertical growth and to a lesser extend to lateral expansion of vegetation on the landforms under construction. *In situ* root excavations demonstrated the systematic formation of numerous adventitious roots that explore the new layers of sediment (Corenblit et al., 2018) – with a tropism linked to the higher organic level as observed on the Allier River by Ding (2014). At the same time the dense network of adventitious roots combined to the structural roots increase the resistance of individuals to uprooting. In the current context, the recurrent massive trapping of fine sediments seems to improve the anchoring, growth and resistance performance of *P. nigra* populations to floods with a return period of twenty years.

No significant vegetation destruction was observed on the Garonne following vicennial floods since the 1990s. These biogeomorphological units are functional from an ecological point of view because at the population scale *P. nigra* is able (i) to strengthen its own inherent ability to resist hydrogeomorphological disturbances and thus is able to grow to sexual maturity in favourable conditions, and (ii) to strengthen its resilience capacity resulting from successful sexual reproduction through the facilitation effect offered by the upstream more mature cohorts.

However, the very strong spatial expansion by *P. nigra* , in a context of channelization that no longer allows the channel to sufficiently erode its banks, has led, after thirty years, to a very imminent situation of blocking of the biogeomorphological succession in the post-pioneer and mature stages with reducing possibility of rejuvenation and regeneration of open alluvial surfaces (Corenblit et al., 2016b). It was suggested that only a very exceptional flood with a return period of about 100 years may be able to reset the succession today.

The observations of *P. nigra* population and landform dynamics on the Garonne River are concordant with the concept of biogeomorphological life cycle (BLC) proposed by Corenblit et al. (2014). The BLC model applies at the population level and aligns with the concept of positive niche construction *sensu* Odling-Smee et al. (2003). Natural selection acting on riparian trees over their life cycle would, over the long term, lead to an increased probability of survival and sexual reproduction in individuals exhibiting suitable trait variations (Corenblit et al., 2009b, 2020b). The fluvial environment, characterized by strong physical constraints, exerts a predominant selective pressure on riparian trees. However, the influence of riparian trees on the hydrogeomorphological components of their environment can modulate this pressure throughout the life cycle. Indeed, the life history of poplars in a riparian context consists of a succession of characteristic developmental phases where physical components of the hydrogeomorphological environment and biological characteristics of riparian trees interact (Corenblit et al., 2014a). The establishment of a population of *P. nigra* on exposed sediment surfaces is not an exclusively unidirectional process in which seedlings solely undergo physical selection pressures. The feedback dynamics between*P. nigra* trait values and population physiognomy and geomorphology during its life cycle lead to the emergence of biogeomorphic entities in the river corridor, such as vegetated fluvial islands, bars and wooded floodplains. The BLC describes the fundamental phases of propagule dispersal, recruitment, and establishment up to the sexual maturity *of*

P. nigra , outlining the hierarchy of interactions and feedbacks between biotic and abiotic components during these phases. This model elucidates how the modification of the hydrogeomorphological environment by the black poplar enhances its fitness (determined by its survival, growth, and sexual reproduction), resulting in a positive niche construction.

Hosted file

`image4.emf` available at https://authorea.com/users/701832/articles/688065-fluvial-biogeomorphological-feedbacks-from-plant-traits-to-the-landscape-lessons-from-french-rivers-in-line-with-a-m-gurnell-s-influential-contribution

Figure 4: Observed feedback at the population level. (a) Established dense pioneer black poplar cohort with a very high growth rate on a gravel bar of the Garonne River; (b) same cohort in winter, with well-distinguishable massive sediment trapping in the vegetation unit. Photographs: Dov Corenblit.

Community-level feedbacks: responses and effects of biodiversity on the functioning of riverine ecosystems

At the community level, riparian vegetation can decisively modulate fluvial dynamics, and in return, adjusts its structure (floristic composition, physiognomy and mean trait value) to new environmental configurations evolving under biotic control according to characteristic resilient succession patterns. Research carried out on the Tech and Allier Rivers permitted to identify, at the community level, a number of key elements of the abiotic-biotic feedback which control the structure and functioning of riverine ecosystems in different and more or less artificialized hydrogeomorphological contexts. As suggested by Tilman (1996), Loreau et al. (2001; 2021) and Hooper et al. (2005), our investigations showed that the diversity of response and effect traits of engineer organisms influences the functioning and stability or resilience of the ecosystem (Fig. 5).

4.1. Function of herbaceous plants: facilitation and resilience

Fieldwork carried out on the Tech River, South France, that is, in a Mediterranean-mountainous torrential context, has highlighted the functional role of herbaceous formations on alluvial bars (Corenblit et al., 2009a). According to the hydrosedimentary regime, herbaceous units may be able to induce a facilitation effect for the recruitment and survival of herbaceous and woody seedlings and promote the resilience of plant biodiversity on exposed alluvial bars through habitat stabilization and seed trapping. In the case of the Tech River, vegetation starting at the herbaceous stage on highly exposed gravel surface, had a very significant impact on surface sediment dynamics and the seed bank, i.e., the set of seeds contained in the substrate, which may contribute to the ecological and biogeomorphological resilience of the river system.

Dense herbaceous structures colonizing the most exposed areas of alluvial bars protected fine substrate very effectively from erosion during floods. Once established, living herbaceous structures, even senescent or dead, contributed recurrently, every year, to the deposition of new layers of sandy-silty sediments (on average 3 cm yr^{-1}). These deposits occurred mainly at the edge of the main channel and secondary channels during quasi-annual morphogenic torrential floods where the erosion process is normally dominant on coarse-grained surfaces. The structure of the seed bank had been described in detail under a binocular microscope in the laboratory LEFE, Toulouse, from numerous sediment samples taken in the deposition zones. The deposition of very numerous seeds (sometimes up to 1,000 seeds and 50 species per 10 cm^3 sample) accompanied this process of stabilization and retention of fine sediments at the top surface of the gravel bars near the water resource. Erosion (on average 20 cm yr^{-1}) measured in the adjacent areas with low plant cover suggested that the herbaceous cover locally represented a critical parameter which controlled the threshold of mobilization of coarse sediment, surface deposition, and the stabilization of fine sediment.

The action of herbaceous structures on sediment dynamics had so far been neglected in high energy fluvial contexts. However, it turned out to play an important ecological role in promoting the resilience of plant biodiversity on alluvial bars that are regularly swept by floods and strongly constrained in summer by possible severe temperatures and hydric stress. This process is similar to the development of a regeneration niche under strong biotic control (Lavorel and Chesson, 1995; Grubb, 1997; Silvertown, 2004). It seems appropriate to establish here the relationship with the facilitation process in constrained environments as described by Bertness and Callaway (1994) and Bruno et al. (2003).

The facilitation process self-sustains itself as long as a large torrential flood does not destabilize the entire vegetation-sediment complex. In some locations on alluvial bars, a few native herbaceous species (e.g., *Polygonum lapathifolium* , *Echinocloa crus-galli*) and exotic species (e.g., *Cyperus eragrostis* ,*Bidens frondosa* , and *Paspalum paspalodes*) with high abundance alone fulfilled the function of stabilizing and retaining fine sediments and seeds. However, in most cases, this function was ensured at the community scale by a multitude of opportunistic herbaceous species with low abundance that form a heterogeneous, dense, and complex mat structure due to its architectural and biomechanical characteristics. This latter observation suggests that the combination of different morphological groups and biomechanical abilities of herbaceous plants, or even life histories, within the same plant unit positively influenced the resistance and resilience of the entire vegetation structure to hydraulic constraints and the effectiveness of sediment and seed retention.

The areas subjected to the effects of herbaceous formations also represented a favourable support for the initiation of the niche construction process by pioneer woody vegetation as well as the associated herbaceous plant succession. These biogeomorphological units with an herbaceous cover and an associated layer of fine sediments offered more favourable habitat conditions for the summer survival of seedlings of *P. nigra* , *Salix* spp., and *Alnus glutinosa* . Herbaceous units on the edge of the channel showed a tendency to evolve in less than three years – at least in the absence of a too large flood – towards dense pioneer shrub formations dominated on the Tech by the three pioneer riparian species mentioned above. These mixed herbaceous/shrub pioneer units (between 2 and 3 m in average height three years after their recruitment) have a very high surface roughness and remained perfectly in place during the flash floods via a very high biomechanical resistance of the woody structures. In addition, they showed a strong resilience of the herbaceous floristic structure constituting the lower layer, i.e., the local seed bank and new seed inputs during floods permitting recovery.

4.2. Function of woody plants: biogeomorphological succession and niche construction

After their establishment on alluvial bars, following the critical recruitment phase sometimes facilitated by herbaceous formations, pioneer woody riparian plants act as ecosystem engineers by trapping large amounts of fine sediments. Studies conducted on the Tech, Garonne and Allier Rivers have shown that pioneer woody riparian vegetation is a predominant factor in the stabilization and construction of habitat and plant succession in dynamic riparian environments.

For example, on the Tech River, Corenblit et al. (2009a) observed a strong correlation between net annual sedimentation rates and the intercepted plant biovolume by floods. In the Allier River fluvial corridor, biotic-abiotic feedbacks also occurred between pioneer woody vegetation that is strongly influenced by hydrogeomorphological constraints (sediment transport and deposition, shear stress, hydrological variability) and fluvial geomorphology which is itself modulated by established vegetation. Hortobágyi et al. (2018a) studied 16 alluvial bars on the Allier River in the Natural National Reserve of the Val d'Allier (RNNVA) to assess the ability of three pioneer riparian engineer species (*P. nigra* , *S. purpurea* and*S. alba*) to establish and act as ecosystem engineers by trapping sediments and building/stabilizing fluvial forms on alluvial bars. The objective was to identify empirically the preferential establishment window (recruitment and establishment zones) of these three engineer species, as well as their biogeomorphological feedback window (zones where these species act significantly on geomorphology). The results showed that the establishment and feedback windows of the three species varied significantly along the longitudinal profile of alluvial bars, namely that relating to the upstream-downstream exposure to hydrogeomorphological flows, as well as along the transverse gradient, i.e., the gradient of hydrological connectivity from the main water channel to the floodplain. At the bar scale, the evolution of fluvial landforms was controlled differentially according to the morphological and biomechanical attributes of each of the three species. These latter exhibited an inherent (genotypical) variation modulated according to age and degree of exposure on the bar (phenotypic plasticity).

In the current hydrogeomorphological context of the Allier River,*P. nigra* is the most abundant pioneer woody species and is the dominant engineer species. It affects the geomorphological dynamics at the scale of the entire alluvial bars, except in their upstream part where individuals remain small due to the direct exposure to very high hydrodynamic forces. *S. purpurea* established and acted as an ecosystem engineer in the most exposed locations of the alluvial bars, i.e., upstream and near the main channel. *S. alba* established in the downstream areas of the bars, near the secondary channels, and affected the geomorphology within patches of mixed vegetation with*P. nigra* and *S. purpurea* . The establishment and feedback windows of the three engineer species also overlapped in places, especially in the intermediate part of the bars. Thus, the total establishment and feedback window of the three species corresponds to a larger spatial extent than that defined individually by each species on the alluvial bars. This study highlighted the role of the diversity of functional response and effect traits of riparian engineer species and the extent of niche construction by these three species along hydrogeomorphological gradients.

On the Tech River, Corenblit et al. (2009a) observed peaks in specific diversity and abundance in the seed bank within post-pioneer woody units that are less directly exposed to hydrogeomorphological flows than alluvial bars. This was explained by a large amount of floating seeds that were deposited there during quasi-annual flood peaks following the low water level, low flow velocities, and high plant roughness. Floristic distance analyses based on species presence-absences at the surface and in the seed bank indicated that, unlike the areas immediately adjacent to the water channels on alluvial bars, a very small percentage of this diversity contained in the seed bank was expressed at the surface. The resistant seeds remained in part in dormancy in the substrate. This result suggests that post-pioneer biogeomorphological units forming a riparian forest partially disconnected from hydrogeomorphological perturbations (post-pioneer fluvial islands and floodplain) potentially fulfil a function as a reservoir of plant diversity at the scale of the corridor. The storage, or accumulation of seeds, could contribute to ensure the ecological resilience of plants following low-frequency, high-amplitude flow disturbances that cause massive destocking and maximum seed dispersal within the fluvial corridor.

In a study of the seed bank on the Allier River, Corenblit et al. (2016a) demonstrated that pioneer woody individuals of *P. nigra*and *Salix* spp. that establish on the alluvial coarse-grained bars of this high-energy river promote the retention of fine sediment during quasi-annual floods, within their stands and just downstream in the form of sediment tails, i.e. obstacle marks. The retention of fine sediment is accompanied by the deposition of a large number of seeds transported by the flow, i.e., by hydrochory. Here, the hypothesis was validated that, on exposed alluvial bars, pioneer riparian trees, either isolated or growing in dense groups, form obstacles to flow and predominantly control the deposition of seeds within sediment tails composed of fine sands and silts depositing on a gravel surface. The structure of the seed bank was described in detail at the binocular microscope in the laboratory and from a germination test performed in a greenhouse. It was compared between samples collected in the sediment tails and control samples collected on the bare surfaces of the alluvial bars. At the surface (at 2 cm depth), the abundance of seeds and species richness were significantly higher in areas subjected to the tree obstacle (number of seeds N: 693 $\pm$ 391; number of species S: 17 $\pm$ 3) than on bare surfaces (N: 334 $\pm$ 371; S: 13 $\pm$ 5). Surface and sub-surface samples (at 20 cm depth) were also significantly different, with the sub-surface samples being almost devoid of seeds (N: 514 $\pm$ 413, S: 15 $\pm$ 5 and N: 3 $\pm$ 6; S: 1 $\pm$ 2).

These results suggest a biogeomorphological feedback loop between sediment dynamics controlled by riparian trees, the retention of associated seeds, and the growth of herbaceous formations from these seeds. This feedback loop is complex and involves, in a first step, the process of hydrochory and sediment retention by trees; in a second step, the growth of herbaceous vegetation on sediment tails and the local dispersion of seeds by barochory; and in a final step, the contribution of herbaceous formations to the stabilization and construction of the sediment tail during quasi-annual floods. Corenblit et al. (2016b) have demonstrated that this feedback loop promotes the resistance and resilience of herbaceous plant diversity on the bars of the Allier River.

Altogether, the results of these *in situ* studies on the Tech, Garonne and Allier Rivers, targeting vegetation on the surface and in the seed bank, highlight a characteristic and recurring correlation between geomorphological adjustments and growth, physiognomy and plant composition on the surface and in the seed bank. The floristic structure in the seed bank and on the surface, the plant physiognomy and the distribution of strategies along the longitudinal and transversal gradients of disturbance do not result from a unidirectional effect of the hydrogeomorphological compartment, but rather from a feedback loop with the hydrogeomorphological components under biotic control.

The process of sediment accretion within pioneer plant structures leads to a transition from a phase dominated by hydrogeomorphological processes, in which seeds and seedlings are unidirectionally subjected to physical constraints (submersion, erosion, sedimentary burial, water table fluctuations), to a phase where abiotic-biotic interactions are multiple, intense, and bidirectional. These pioneer units dominated by opportunistic strategies evolve into more robust post-pioneer tree units in just a few years (between 4 and 5 years), reach an average height of 7 m and develop on topographically raised surfaces due to the rapid accretion of sand and silt. This phase, which is generally transient, is characterized by strong landscape heterogeneity and high plant diversity at the scale of the bar. In just a few years and the absence of destruction caused by an exceptional flood or lateral erosion due to channel displacement, abiotic-biotic feedbacks drive biogeomorphological units towards a more stable and ecologically mature phase, which is more resistant to hydrogeomorphological disturbance events, physiological stress and invasion by exotic species (Corenblit et al., 2014b). Within these units, partially disconnected from frequent flood events, sediment deposits become negligible for quasi-annual floods. At this stage, competitive strategies take over in terms of floristic structure and plant diversity decreases sharply due to the exclusion of many opportunistic herbaceous species. Within the cycle of fluvial landform construction and plant succession, this stage represents a biogeomorphological "attractor". It coincides with the formation of post-pioneer and mature fluvial islands (*sensu* Gurnell et al., 2018a, 2002) and alluvial floodplains supporting softwood species and, possibly at the end of the cycle, hardwood species.

Hosted file

`image5.emf` available at https://authorea.com/users/701832/articles/688065-fluvial-biogeomorphological-feedbacks-from-plant-traits-to-the-landscape-lessons-from-french-rivers-in-line-with-a-m-gurnell-s-influential-contribution

Figure 5: Observed feedback at the community level. (a) Herbaceous and arboreous communities in the active tract of the Tech River and (b) the Allier River. Photographs: Dov Corenblit (a) and Franck Vautier (b).

Landscape-level feedbacks: biological *versus* physical forcing in contrasted hydrogeomorphological contexts

At the scale of the fluvial landscape, our research was carried out primarily on the Tech, Allier and Isère Rivers, using two and three-dimensional spatiotemporal analyses with GIS, stereo and multi-image photogrammetry and LiDAR. These three rivers differ in their morphodynamics and the level of anthropogenic pressure. The Tech is a Mediterranean torrential river with a very irregular hydrogeomorphological regime. Anthropogenic pressure has led to channel bed vertical incision, lateral stabilization of its banks and therefore to a certain loss of dynamics despite the virulence of flash floods. The Allier is a high-energy river that is, in its lower section (RNNVA) still relatively free to move laterally in a wide meander belt. The Isère River is a high-energy river that has was laterally confined with huge embankments. This resulted in a channel mostly straightened and migrating alternate bars progressively stabilizing and heavily colonized by vegetation.

Spatial analyses of the feedback between colonization/vegetation succession dynamics and landscape/fluvial style dynamics on these three rivers have made it possible to highlight different types of responses and effects of riparian vegetation at the landscape scale and thus to estimate the impact of local feedbacks (at the scale of traits and population) on the organization of the habitat mosaic over few decades (Fig. 6).

5.1. The Tech River landscape: dominance of biotic forcing in an extremely irregular torrent context

A spatially explicit retrospective GIS analysis of the landscape dynamics of the Tech River, from a situation of complete abiotic reinitialization at the scale of the fluvial corridor – following the catastrophic flood of October 1940 – made it possible to specify the intensity and spatial modalities of responses and effects of vegetation on fluvial morphodynamics in a hydrologically irregular torrential Mediterranean context with moderate anthropogenic pressure (Corenblit et al., 2010).

The hydrological configuration (no major floods for ten years) that followed immediately after the devastating flood of 1940 allowed to clearly distinguish two modalities of plant succession specifically in relation to the effect of close location to the water resource on the growth rate and density of plant cover. Distance and relative altitude from main and secondary channels acted in this Mediterranean context as key parameters controlling vegetation growth rates. Indeed, (i) close to channels and the water resource, in low-lying areas, plant growth/succession is strongly stimulated. Dense tree formations develop in less than ten years; the stimulation and success of the recruitment of pioneer herbaceous and woody species that were measured at the local scale on alluvial bars in the highly exposed zones (Corenblit et al., 2009a) corroborate and clarify the processes underlying these dynamics. (ii) Far from wet channels, plant growth/succession is slower and follows a more progressive successional trajectory through a shrubby and sparse tree stage that lasts about thirty years. A dendrochronological analysis of adult *P. nigra* individuals growing close to and far from the active channel showed a contrast in the growth rate of the rings (on average 1.3 cm of annual growth at the edge of the channel against 0.4 cm far from it). During this period, avulsions favoured by the dense tree band at the edge of the channel led to the rejuvenation of succession over a significant area of the corridor (about 40%). When the floodplain was covered with a dense forest after thirty years, the system switched to a new domain of stability because the rejuvenation process was strongly constrained at the scale of the entire corridor, even for morphogenic floods with a return period of between twenty and thirty years. The active tract (active channel and bare alluvial bars) then contracted and the channel incised, potentially irreversibly in the absence of an exceptional flood with a frequency >100 years.

It appears that the relationship between the speed, quality, and location of vegetation closure and the frequency/amplitude of floods determines the conditions of geomorphological equilibrium at the scale of the corridor. The combined effect of the two modalities of plant succession favours the progression of the riparian forest within the entire fluvial corridor (from the outside to the inside and vice versa) and the contraction and confinement of the active tract. The spatial configuration which results from biotic-abiotic feedbacks after thirty years on the Tech represents a biogeomorphological attractor state. The shift of the geomorphological equilibrium system towards stabilization is explained by the fact that, although plant growth is slower on the floodplain, a dense tree formation eventually develops at the medium term (30 years on the Tech), thus reducing the probability of destruction by floods. The areas near the channel are frequently flooded, but the growth of vegetation well adapted to hydraulic constraints is stimulated there. The very rapid and efficient development of pioneer vegetation in the backwater along the active channel maintains the continuity of the coupling with sediment accretion processes and thus minimizes the width of the active band while the floodplain becomes progressively more densely wooded. This type of phenomenon is involved when a river evolves from an unstable braiding style to a more simplified and entrenched stable style.

5.2. Isère River landscape: dominance of biological forcing in-between dikes in a highly anthropized context

The intricate interplay between hydrogeomorphological processes and riparian vegetation can play a pivotal role in shaping the fluvial landscapes within highly-confined rivers. Corenblit et al. (2020a) studied the reciprocal coupling between river morphodynamics and vegetation succession in the Isère River, France, where human intervention in the form of lateral confinement with embankments and straightening had a transformative impact on riverine landscape dynamics (see also Vautier, 2000; Vautier et al., 2002).

Using GIS analysis of historical aerial photographs spanning nearly five decades, from 1948 to 1996, the authors showed that a remarkable biogeomorphological transformation unfolded as the once mobile transverse gravel bars began a gradual but significant colonization by a diverse array of vegetation types. This situation presented an opportunity to understand the temporal adjustments between fluvial landforms and vegetation succession stages, ultimately culminating in the establishment of mature riparian forests on stabilized alternate bars. This biogeomorphological trajectory of change was a direct consequence of feedbacks between hydraulics, sediment transport, and vegetation dynamics in a highly impacted river reach. The mosaic of vegetated bars that emerged was an outcome of the strong bioconstruction and biostabilization effects exerted by pioneer vegetation on bars of differing ages, sizes, and mobility within the riverine landscape.

Field measurements undertaken in 1996 provided tangible evidence of a robust positive feedback loop between sediment dynamics and the ongoing riparian vegetation succession (Vautier, 2000). In the complex balance between physical and biotic adjustments, the vegetated bars evolved as emergent biogeomorphological entities specifically resulting from the biogeomorphological feedbacks of sediment accretion, topographic raise, and vegetation growth and succession. Co-inertia analysis (CoIA), a type of ordination statistical technique used for exploring and understanding bi-directional relationships between two or more data tables or matrices, permitted the quantification of the intricate relationships. A highly significant statistical association between geomorphological and vegetation variables (as exemplified by an RV value of 0.41, $p < 0.001$) was found. This association explained a staggering 95% of the variability along just one axis, demonstrating the existence of an exceedingly robust feedback loop between geomorphological changes and vegetation succession.

To appreciate the full significance of these findings, we must turn our gaze to the broader context of the theoretical model of fluvial biogeomorphological succession based on positive feedback loops between fluvial morphodynamics and vegetation succession (FBS model; Corenblit et al., 2007). The empirical observations from the Isère and Tech Rivers both allowed the validation of the FBS model, suggesting that this model is applicable to natural but also channelized rivers.

5.3. Allier River landscape: dominance of physical forcing in a context with a more regular disturbance regime

The biogeomorphological dynamics of the Allier River at the landscape scale contrast with those of the Tech and Isère Rivers, where vegetation act as an important factor of stabilisation in the active tract. On the Allier River, hydrogeomorphological processes still seem to be dominant within the active tract over the effect of vegetation on the structuring of the habitat mosaic, due to a more regular high disturbance regime and strong lateral bank erosion dynamics ensured by the translations of the main channel during bankfull floods (Garófano-Gómez et al., 2017). However, the hydrogeomorphological conditions in the Allier River are presently undergoing changes.

At the scale of the fluvial corridor, Hortobágyi et al. (2018b) showed that the vegetation classes with the lowest height are concentrated hundred meters away from the main channel and at higher elevations, about 3-4 m. These results do not apparently match with the theoretical FBS model (Corenblit et al., 2007), in which the age of the vegetation increases with increasing distance from the main channel and relative elevation. On the Allier River, the development of low shrub vegetation hundred meters away from the main channel is the result of a secondary "dry" succession dominated by *Prunus* spp. on floodplain surfaces today disconnected from frequent floods that are also subject to grazing. The fact that mature large-sized tree vegetation is located near the main channel suggests that the preferential areas for rejuvenation of the plant succession and associated fluvial forms are located along the point bars in the meander concavities.

The tallest vegetation classes are located further upstream on the bars, near the main channel. This is explained by the fact that the channel is migrating very actively and progressively towards the opposite bank and the bars are migrating downstream. Surprisingly, the difference between the average elevation of bare and vegetated bar surfaces is not significant. The vegetation cover is concentrated around 0.5 m above the low water level, while the bare substrate is concentrated below 0.5 m and at around 1 m of elevation. The occurrence of these open bare surfaces at higher elevations relative to the low water level seems to reflect an unsuccessful recruitment of pioneer riparian woody vegetation, including *P. nigra* , on these surfaces too much disconnected from the surface and alluvial water pools.

At the bar scale, on the Allier River, the biogeomorphological succession model was rather supported by these results. The classes with highest vegetation reflecting the mature stage within the vegetation succession were indeed located at a higher altitude. However, the average elevation of the vegetation height classes of 5-10 m and > 10 m do not vary and therefore do not have a very specific topographic signature. The maximum sediment trapping effect is probably reached when the height of the vegetation is around 5-10 m, or about 4-8 years after recruitment. These observations are in good agreement with the observations on the Garonne River for *P. nigra*cohorts. The most important physiognomic changes in *P. nigra*(loss of the multi-stemmed shrub architecture in favour of a single large trunk) occur during this rather early growth phase. From 15 m in height, the density of *P. nigra* stems decreases drastically and their diameter increases very significantly. These physiognomic changes result from the reduction of the exposure of individual plants to hydrogeomorphological constraints, partly thanks to biotically controlled sediment accretion and the protective effect of individuals against each other. The maximum occurrence of tall arboreous structures at the scale of the bar is currently located on the Allier from 0.5 to 1 m above the low water level. The observed elevation of the classe with the highest vegetation on the Allier River is consistent with observations on other high-energy rivers, such as the Tagliamento River in Italy (Bertoldi et al., 2011) and the Santa Maria River in the United States (Kui et al., 2014; Manners et al., 2015). In these rivers, the highest topographic levels are associated with intermediate canopy height classes (1-5 m and 5-10 m). However, on the Allier River, the highest topographic levels are associated with canopy heights of 5-10 m and > 10 m. A possible explanation of this distributional pattern of vegetation height classes is that the rate of sediment accumulation by the pioneer vegetation varies depending on the type of river, sediment load, and hydrogeomorphological regime. The Allier River has a substantial sediment load, which could result in a significant sediment trapping effect caused by pioneer vegetation in the form of successive parallel lines along the water channel in the Allier River. This phenomenon could potentially account for the increased elevation in the 5-10 m and > 10 m height classes.

However, Garófano-Gómez et al. (2017) analysed the vegetation succession based on eight sets of aerial images of the riparian corridor spanning from 1967 to 2014 and its relation with the Allier River flow regime. The results indicated that between 1967 and 2005, the study area exhibited a shifting habitat pattern. After 2005, there was a significant decrease in progression and retrogression processes, leading to increased stability, with no more channel migration and patches no longer experiencing either progression or retrogression. This study highlights a distinct turning point in succession processes at the beginning of the 21st century with a contraction of the active tract resulting from a decrease in flood frequency and magnitude. The biogeomorphological interaction between vegetation and geomorphology is likely to adapt in the near future, with the increasing influence of plants on landform stabilization and development.

Hosted file

`image6.emf` available at https://authorea.com/users/701832/articles/688065-fluvial-biogeomorphological-feedbacks-from-plant-traits-to-the-landscape-lessons-from-french-rivers-in-line-with-a-m-gurnell-s-influential-contribution

Figure 6: Observed feedback at the community mosaic level. (a) Community mosaic of the Allier River with a predominant physical signature and (b) the Isère River with a predominant biotic signature on the alternate bars in the active tract.

Conclusion

The here presented results from various biogeomorphological investigations on French rivers underpin the important role played by riparian vegetation in such riverine ecosystems of the temperate zone in modulating hydrogeomorphological processes and fluvial landforms, as early advocated by Angela M. Gurnell. Her essential suggestions, having led at the time to some controversies, are now widely accepted and, as shown here, refined at different spatiotemporal scales as well as different ecosystem levels, from the individual/micro-form to the community mosaic/fluvial style.

Today, the fluvial biogeomorphological lessons learned from the French rivers, in addition to other studies in France, Europe and overseas, open new perspectives in the comprehensive study of riverine systems and their management considering feedback mechanisms between water, sediment and riparian plants. The here presented results, often obtained in close collaboration with Angela M. Gurnell, point to the need to better quantify, understand and model feedbacks between river morphodynamics and vegetation at nested spatiotemporal scales as well as its resilience aptitudes to disturbances. Indeed, the resilience of rivers may largely dependent on feedbacks between hydrogeomorphology and the dynamics of engineer populations, such as black poplar. Its comprehension, based on the biogeomorphological approach advocated, is needed to better predict future river evolutionary trajectories in the light of human pressures as well as restoration measures, climate and global change.

In addition, the different methods and approaches employed here and observations made, clearly helped, over the last twenty years, to contribute to the enlargement of the discipline of geomorphology to ecology and also to evolutionary ecology, endorsed by the biogeomorphological approach.

Conflict of Interest Statement

No conflict of interest.

References

Amoros, C., Petts, G.E. (Eds.). (1993). *Hydrosystèmes fluviaux.*Collection d'Écologie, Masson, Paris.

Barsoum, N. (2002). Relative contributions of sexual and asexual regeneration strategies in *Populus nigra* and *Salix alba*during the first years of establishment on a braided gravel bed river.*Evol. Ecol., 15* , 255–279.

Bendix, J., & Hupp, C.R. (2000). Hydrological and geomorphological impacts on riparian plant communities. *Hydrol. Process., 14* (16–17), 2977–2990.

Bertness, M.D., & Callaway, R. (1994). Positive interactions in communities. *Trends in Ecology & Evolution, 9* , 191-193.

Bertoldi, W., Gurnell, A.M., & Drake, N.A. (2011). The topographic signature of vegetation development along a braided river: results of a combined analysis of airborne lidar, color air photographs, and ground measurements. *Water Resources Research, 47* , 1-13.

Bornette, G., & Puijalon, S. (2011). Response of aquatic plants to abiotic factors: a review. *Aquatic Sciences, 73* , 1-14.

Bornette, G., Tabacchi, E., Hupp, C., Puijalon, S., & Rostan, J.C. (2008). A model of plant strategies in fluvial hydrosystems.*Freshwater Biology, 53* , 1692-1705.

Bruno, J.F., Stachowicz, J.J., & Bertness, M.D. (2003). Inclusion of facilitation into ecological theory. *Trends in Ecology & Evolution, 18* , 119–125.

Corenblit, D., Steiger, J., & Tabacchi, E. (2010). Biogeomorphic succession dynamics in a Mediterranean river system. *Ecography, 33* , 1136-1148.

Corenblit, D., Steiger, J., Mazal, L., & Till-Bottraud, I. (2020b). Relier la biogéomorphologie fluviale à l'écologie évolutive : un focus sur les arbres riverains pionniers. *Géomorphologie, relief, processus, environnement, 26* , 55-72.

Corenblit, D., Tabacchi, E., Steiger, J., & Gurnell, A. (2007). Reciprocal interactions and adjustments between fluvial landforms and vegetation dynamics in river corridors: a review of complementary approaches. *Earth-Science Reviews, 84* , 56-86.

Corenblit, D., Vautier, F., González, E., & Steiger, J. (2020a). Feedbacks between fluvial landforms and riparian vegetation succession: the channelized Isère River, France, a flume analogue. *Earth Surface Processes and Landforms, 45* , 2020-2035.

Corenblit, D., Steiger, J., Gurnell, A.M., & Naiman, R.J. (2009b). Plants intertwine fluvial landform dynamics with ecological succession and natural selection: a niche construction perspective for riparian systems. *Global Ecology and Biogeography, 18* , 507-520.

Corenblit, D., Steiger, J., Gurnell, A., Tabacchi, E., & Roques, L. (2009a). Control of sediment dynamics by vegetation as a key function driving biogeomorphic succession within fluvial corridors. *Earth Surface Processes and Landforms, 34* , 1790-1810.

Corenblit, D., Davies, N., Steiger J., Gibling, M., & Bornette, G. (2014c). Considering river structure and stability in the light of evolution: feedbacks between riparian vegetation and hydrogeomorphology.*Earth Surface Processes and Landforms, 40* , 139-207. (Invitation par l'éditeur en chef de ESPL pour un "State of Science").

Corenblit, D., Steiger, J., Tabacchi, E., González, E., & Planty-Tabacchi, A.M. (2014b). Ecosystem engineers modulate exotic invasions in riparian plant communities. *River Research and Applications, 30* , 45-59.

Corenblit, D., Vidal, V., Cabanis, M., Steiger, J., Garófano-Gómez, V., Hortobágyi, B., Otto, t., Roussel, E., & Voldoire, O. (2016a). Seed retention by pioneer trees enhances plant diversity resilience on gravel bars: Observations from the river Allier, France. *Advances in Water Resources, 93* , 182-192.

Corenblit, D., Steiger, J., González, E., Gurnell, A.M., Charrier, G., Darrozes, J, Dousseau, J, Julien, F., Lambs, L., Larrue, S., Roussel, E., Vautier, F., & Voldoire, O. (2014a). The biogeomorphological life cycle of *Populus nigra L.* during the fluvial biogeomorphological succession. *Earth Surface Processes and Landforms, 39* , 546-563.

Corenblit, D., Baas, A., Balke, T., Bouma, T., Fromard, F., Garófano-Gómez, V., González, E., Gurnell, A.M., Hortobágyi, B., Julien, F., Kim, D., Lambs, L., Stallins, J.A., Steiger, J., Tabacchi, E., & Walcker, R. (2015). Engineer pioneer plants respond to and affect geomorphic constraints similarly along water-terrestrial interfaces worldwide. *Global Ecology and Biogeography, 24* , 1363-1376.

Corenblit, D., Steiger, J., Charrier, G., Darrozes, J, Garófano-Gómez, V., Garreau, A., González, E., Gurnell, A.M., Hortobágyi, B., Julien, F., Lambs, L., Larrue, S., Otto, T., Roussel, E., Vautier, F., & Voldoire, O. (2016b). *Populus nigra L.* establishment and fluvial landform construction: biogeomorphic dynamics within a channelized river. *Earth Surface Processes and Landforms, 41* , 1276-1292.

Corenblit, D., Till-Bottraud, I., Garófano-Gómez, V., González, E., Hortobágyi, B., Julien, F., Lambs, L., Otto, T., Roussel, E., Steiger, J., & Tabacchi, E. (2018). Niche construction within rivers: The unexplored role of intra-specific positive interaction in Salicaceae trees. *Geomorphology, 305* , 112-122.

Diehl, R.M., Merritt, D.M., Wilcox, A.C., & Scott, M.L. (2017). Applying functional traits to ecogeomorphic processes in riparian ecosystems. *Bioscience, 67* (8), 729-743.

Ding, Z. (2014). Réponse du système racinaire de *Populus nigra L.*aux contraintes hydrogeomorphologiques sur les bancs alluviaux de la rivière Allier. *Master thesis, Université Blaise Pascal* , 57 p.

Edwards, P.J., Kollmann, J., Gurnell, A.M., Petts, G.E., Tockner, K., & Ward, J.V. (1999). A conceptual model of vegetation dynamics on gravel bars of a large Alpine river. *Wetlands Ecology and Management, 7* , 141-153.

Francis, R.A., Corenblit, D., & Edwards, P.J. (2009). Perspectives on biogeomorphology, ecosystem engineering and self-organisation in island-braided fluvial ecosystems. *Aquatic Sciences, 71* , 290-304.

Francis, R.A., & Gurnell, A.M. (2006). Initial establishment of vegetative fragments within the active zone of a braided gravel-bed river (River Tagliamento, NE Italy). *Wetlands, 26* (3), 641-648.

Garófano-Gómez, V., Corenblit, D., Moulia, B., González, E., & Steiger, J. (2018). Phenotypic plasticity of *Populus nigra* to hydrogeomorphological constraints: A trait-based approach. *ECOVEG 14 - Écologie des Communautés Végétales* , 24-26 avr. Toulouse (France).

Garófano-Gómez, V., Metz, M., Egger, G., Díaz-Redondod, M., Hortobágyi, B., Geerling, G., Corenblit, D., & Steiger, J. (2017). Vegetation succession processes and fluvial dynamics of a mobile temperate riparian ecosystem: the lower Allier River (France). *Géomorphologie, relief, processus, environnement, 23* , 187-202.

Gonzalez, E., Corenblit, D., Garófano-Gómez, V., Henry, A., Martinez-Fernandez, Shafroth, P., & Sher, A. (2018). Regeneration of Salicaceae riparian forests in the Northern Hemisphere: A New Framework and Management Tool. *Journal of Environmental Management, 218* , 374-387.

Gonzalez, R., et al. (2022). Bringing the margin to the focus: 10 challenges for riparian vegetation science and management. *WIREs Water, 9* , e1604.

Goodson, J.M., Gurnell, A.M., Angold, P.G., & Morrissey, I.P. (2001). Riparian seed banks: structure, process and implications for riparian management. *Prog. Phys. Geog ., 25* (3), 301-325.

Goodson, J.M., Gurnell, A.M., Angold, P.G., & Morrissey, I.P. (2002). Riparian seed banks along the lower River Dove, UK: their structure and ecological implications. *Geomorphology, 47* (1), 45-60.

Grubb, P.J. (1977). The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Review, 52* , 107-145.

Guilloy-Froget, H., Muller, E., Barsoum, N., & Hughes, F.M.R. (2002). Regeneration of *Populus nigra L.* (Salicaceae), seed dispersal, germination and survival in changing hydrological conditions. *Wetlands, 22* , 478–488.

Gurnell, A. (2014). Plants as river system engineers. *Earth Surface Processes and Landforms, 39* (1), 4-25.

Gurnell, A.M. (1995). Vegetation along river corridors: Hydrogeomorphological interactions. In A. Gurnell & G. Petts (Eds.), *Changing River Channels* (pp. 237-260). J. Wiley & Sons Ltd, Chichester.

Gurnell, A.M. (1997). The hydrological and geomorphological significance of forested floodplains. *Global Ecology and Biogeography Letters, 6* , 219-229.

Gurnell, A.M. (2014). Plants as river system engineers. *Earth Surface Processes and Landforms, 39* , 4-25.

Gurnell, A.M., & Grabowski, R.C. (2016). Vegetation-hydrogeomorphology interactions in a low-energy, human-impacted river. *River Research and Applications, 39* , 202-215.

Gurnell, A.M., & Gregory, K.J. (1984). The influence of vegetation on stream channel processes. In International Geographical Union Commission on field experiments in geomorphology. Meeting (pp. 515-535).

Gurnell, A.M., & Gregory, K.J. (1995). Interactions between semi-natural vegetation and hydrogeomorphological processes. *Geomorphology, 13* (1-4), 49-69.

Gurnell, A.M., & Bertoldi, W. (2020). Extending the conceptual model of river island development to different environmental conditions and tree species. *River Research and Applications, 36* (7), 1183-1201.

Gurnell, A.M., & Bertoldi, W. (2022). The impact of plants on fine sediment storage within the active channels of gravel-bed rivers: A preliminary assessment. *Hydrological Processes, 36*

Gurnell, A.M., & Petts, G.E. (2002). Island-dominated landscapes of large floodplain rivers, a European perspective. *Freshwater Biology, 47* (4), 581-600.

Gurnell, A.M., & Petts, G.E. (2006). Trees as riparian engineers: The Tagliamento river, Italy. *Earth Surface Processes and Landforms, 31* , 1558-1574.

Gurnell, A.M., Bertoldi, W., & Corenblit, D. (2012). Changing river channels: The roles of hydrological processes, plants, and pioneer fluvial landforms in humid temperate, mixed load, gravel bed rivers. *Earth-Science Reviews, 111* (1-2), 129-141.

Gurnell, A., Tockner, K., Edwards, P., & Petts, G. (2005). Effects of deposited wood on biocomplexity of river corridors. *Frontiers in Ecology and the Environment, 3* (7), 377-382.

Gurnell, A.M., Bertoldi, W., Francis, R.A., Gurnell, J., & Mardhiah, U. (2018a). Understanding processes of island development on an island braided river over timescales from days to decades. *Earth Surface Processes and Landforms, 44* (2), 624-640.

Gurnell, A.M., Boitsidis, A.J., Thompson, K., & Clifford, N.J. (2006). Seed bank, seed dispersal and vegetation cover: Colonization along a newly-created river channel. *Journal of Vegetation Science, 17* (5), 665-674.

Gurnell, A.M., Goodson, J.M., Angold, P.G., Morrissey, I.P., Petts, G.E., & Steiger, J. (2004). Vegetation propagule dynamics and fluvial geomorphology. In S.J. Bennett & A. Simon (Eds.), *Riparian Vegetation and Fluvial Geomorphology* (Vol. Water and Science Ap). American Geophysical Union.

Gurnell, A.M., Corenblit, D., García de Jalón, D., González del Tánago, M., Grabowski, R.C., O'Hare, M.T., & Szewczyk, M. (2016a). A conceptual model of vegetation–hydrogeomorphology interactions within river corridors. *River Research and Applications, 32* , 142-163.

Gurnell, A.M., Petts, G.E., Harris, N., Ward, J.V., Tockner, K., Edwards, P.J., & Kollmann, J. (2000). Large wood retention in river channels: The case of the Fiume Tagliamento, Italy. *Earth Surface Processes and Landforms, 25* (3), 255-275.

Gurnell, A.M., et al. (2016b). A multi-scale hierarchical framework for developing understanding of river behaviour to support river management.*Aquatic Sciences, 78* , 1-16.

Gurnell, A.M., O'Hare, M.T., Corenblit, D., García De Jalón, D., González Del Tánago, M., Grabowski, R., & Szewczyk, M. (2016). A conceptual model of vegetation-hydrogeomorphology interactions within river corridors. *River Research and Applications, 32* , 142-163.

Gurnell, A.M., O'Hare, M.T., O'Hare, J.M., Scarlett, P., & Liffen, T.M.R. (2013). The geomorphological context and impact of the linear emergent macrophyte, *Sparganium erectum* L.: a statistical analysis of observations from British rivers. *Earth Surface Processes and Landforms, 38* , 1869-1880.

Gurnell, A.M., Petts, G.E., Hannah, D.M., Smith, B.P.G., Edwards, P.J., Kollmann, J., Ward, J.V., & Tockner, K. (2001). Riparian vegetation and island formation along the gravel-bed Fiume Tagliamento, Italy.*Earth Surface Processes and Landforms, 26* (1), 31-62.

Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J., & Wardle, D.A. (2005). Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs, 75* , 3-35.

Hortobagyi, B. (2018b). Multi-scale interactions between riparian vegetation and hydrogeomorphic processes (the lower Allier River) (Doctoral dissertation, Université Clermont Auvergne [2017-2020]).

Hortobágyi, B., Corenblit, D., Steiger, J., & Peiry, J.L. (2018a). Niche construction within riparian corridors. Part I: Exploring biogeomorphic feedback windows of three pioneer riparian species, Allier River, France. *Geomorphology, 305* , 94-111.

Hortobágyi, B., Corenblit, D., ZhuQing, D., Lambs, L., & Steiger, J. (2017). Above- and belowground response of *Populus nigra L.* to mechanical stress within the Allier River, France. *Géomorphologie, relief, processus, environnement, 23* , 219-231.

Jones, C.G., Lawton, J.H., & Shachak, M. (1994). Organisms as ecosystem engineers. *Oikos, 69* , 373-386.

Junk, W.J., Bayley, P.B., & Sparks, R.E. (1989). The flood pulse concept in river-floodplain systems. *Canadian Special Publication of Fisheries and Aquatic Sciences, 106* , 110-127.

Karrenberg, S., Edwards, P.J., & Kollmann, J. (2002). The life-history of Salicaceae living in the active zone of floodplains. *Freshw. Biol., 47* (4), 733–748.

Kui, L., Stella, J.C., Lightbody, A., & Wilcox, A.C. (2014). Ecogeomorphic feedbacks and flood loss of riparian tree seedlings in meandering channel experiments. *Water Resources Research, 50* , 9366-9384.

Lavorel, S., & Chesson, P. (1995). How species with different niches coexist in patchy habitats with local disturbances. *Oikos, 74* , 103-114.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper, D.U., Huston, M.A., Raffaelli, D., Schmid, B., Tilman, D., & Wardle, D.A. (2001). Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science, 294* , 804-808.

Loreau, M., Barbier, M., Filotas, E., Gravel, D., Isbell, F., Miller, S. J., . . . & Dee, L. E. (2021). Biodiversity as insurance: from concept to measurement and application. Biological Reviews, 96(5), 2333-2354.

Lytle, D.A., & Poff, N.L. (2004). Adaptation to natural flow regimes.*Trends Ecol. Evol., 19* (2), 94–100.

Manners, R.B., Wilcox, A.C., Kui, L., Lightbody, A.F., Stella, J.C., & Sklar, L.S. (2015). When do plants modify fluvial processes? Plant-hydraulic interactions under variable flow and sediment supply rates. *Journal of Geophysical Research: Earth Surface, 120* , 325-345.

Merritt, D.M. (2013). Reciprocal relations between riparian vegetation, fluvial landforms, and channel processes. In: J.F. Shroeder, E. Wohl (Editors), *Treatise on Geomorphology, Vol. 9* . Academic Press, San Diego, pp. 219-243.

Moggridge, H.L., & Gurnell, A.M. (2009). Controls on the sexual and asexual regeneration of Salicaceae along a highly dynamic, braided river system. *AQUAT SCI, 71* (3), 305-317.

Muñoz-Mas, R., Garófano-Gómez, V., Doménech, A., Corenblit, D., Egger, G., Francés, F., Ferreira, M.T., García-Arias, A., Politti, E., Rivaes, R., Rodríguez-González, P.M., Steiger, J., Vallés-Morán, F.J., & Martínez-Capel, F. (2017). Exploring the key drivers of riparian woodland successional pathways across three European river reaches.*Ecohydrology, 10* .

Naiman, R.J., & Décamps, H. (1997). The ecology of interfaces, riparian zones. *Annual Review of Ecology and Systematics, 28* , 621-658.

Newbold, J.D., O'Neill, R.V., Elwood, J.W., & Van Winkle, W. (1982). Nutrient spiralling in streams: implications for nutrient limitation and invertebrate activity. *American Naturalist, 120* , 628-652.

O'Briain, R., Corenblit, D., Gurnell, A., & O'Hare, M. (2023). Implications of invasive alien plant species for river hydro-morphodynamics in a changing climate. *WIREs Water* .

O'Hare, M.T. et al. (2016). Plant traits relevant to fluvial geomorphology and hydrological interactions. *River Res. Appl., 32* , 179-189.

Odling-Smee, F.J., Laland, K.N., & Feldman, M.W. (2003). Niche Construction: the Neglected Process in Evolution. *Princeton University Press, Princeton, NJ, USA* .

Paine R.T., 1966. Food web complexity and species diversity.*American Naturalist, 100* , 65-75.

Pickett, S.T.A., & White, P.S. (1985). Natural disturbance and patch dynamics, an introduction. In: Pickett, S.T.A., White, P.S. (Eds.),*The Ecology of Natural Disturbance and Patch Dynamics* . Academic Press, Orlando, pp. 3-13.

Puijalon, S., Bouma, T.J., Douady, C.J., van Groenendael, J., Anten, N.P.R., Martel, E., & Bornette, G. (2011). Plant resistance to mechanical stress: evidence of an avoidance–tolerance trade-off.*New Phytologist, 191* , 1141-1149.

Schnitzler, A., Carbiener, R., & Tremolieres, M. (1992) Ecological segregation between closely related species in the flooded forests of the Upper Rhine Plain. *New Phytologist, 121* , 293-301.

Silvertown, J. (2004). Plant coexistence and the niche. *Trends in Ecology & Evolution, 19* , 605-611.

Southwood, T.R.E. (1977). Habitat, the template for ecological strategies? *Journal of Animal Ecology, 46* , 337-365.

Stanford, J.A., Lorang, M.S., & Hauer, F.R. (2005). The shifting habitat mosaic of river ecosystems. *Verhandlungen der internationalen Vereinigung für theoretische und angewandte Limnologie, 29* , 123-136.

Steiger, J., Corenblit, D., & Vervier, P. (2000). Les ajustements morphologiques contemporains du lit mineur de la Garonne, France, et leurs effets sur l'hydrosystème fluvial. *Zeitschrift für Geomorphologie, 122* , 227-246.

Steiger, J., Gurnell, A.M., Ergenzinger, P., & Snelder, D. (2001). Sedimentation in the riparian zone of an incising river. *Earth Surface Processes and Landforms, 26* , 91-108.

Tockner, K., Malard, F., & Ward, J.V. (2000). An extension of the flood pulse concept. *Hydrological Processes, 14* , 2861-2883.

Townsend, C.R. (1989). The patch dynamics concept of stream community ecology. *Journal of the North American Benthological Society, 8* , 36-50.

Vannote, R.L., Minshall, G.W., Cumins, L.W., Sedell, J.R., & Cushing, C.P. (1980). The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences, 37* , 130-137.

Vautier, F., Peiry, J.L., & Girel, J. (2002). Développement végétal dans le lit endigué de l'Isère en amont de Grenoble : du diagnostic à l'évaluation des pratiques de gestion. *Revue d'Ecologie (Terre Vie) Suppl., 9* , 65–79.

Vautier, F. (2000). Dynamique géomorphologique et végétalisation des cours d'eau endigués : l'exemple de l'Isère dans le Grésivaudan.*PhD thesis, Université Joseph Fourier: Grenoble* .

Ward, J.V. (1989). The four-dimensional nature of lotic ecosystems.*Journal of the North American Benthological Society, 8* , 2-8.

Ward, J.V., Tockner, K., Arscott, D.B., & Claret, C. (2002). Riverine landscape diversity. *Freshwater Biology, 47* , 517-539.

Figure legends

Figure 1. Number of peer reviewed journal articles per year using the combined terms "riparian vegetation" + "geomorphology" + "river*", as archived on Clarivate Web of Knowledge (all databases) (https://www-webofscience-com.inee.bib.cnrs.fr/). A.M. Gurnell's first article using these terms was published in 1997 (see vertical black arrow) and her name comes out first with more than 12% of all articles authored or co-authored. Accessed on 11$^{\text{th}}$ November 2023.

Figure 2: Multi-scale theoretical model of the feedback between riparian vegetation dynamics and river morphodynamics.

Figure 3: Observed feedback at the individual level. (a) PopTrait *ex situ* experiment in Clermont-Ferrand for understanding*P. nigra* responses to biomechanical constraints; (b) sediment tail downstream of a multi-stemmed black poplar on an alluvial bar of the Tech River. The morphology of the sediment tail is correlated with morphological traits of the black poplar individual. Photographs: Virginia Garófano-Gómez (a) and Aurélien Chabanon (b).

Figure 4: Observed feedback at the population level. (a) Established dense pioneer black poplar cohort with a very high growth rate on a gravel bar of the Garonne River; (b) same cohort in winter, with well-distinguishable massive sediment trapping in the vegetation unit. Photographs: Dov Corenblit.

Figure 5: Observed feedback at the community level. (a) Herbaceous and arboreous communities in the active tract of the Tech River and (b) the Allier River. Photographs: Dov Corenblit (a) and Franck Vautier (b).

Figure 6: Observed feedback at the community mosaic level. (a) Community mosaic of the Allier River with a predominant physical signature and (b) the Isère River with a predominant biotic signature on the

alternate bars in the active tract.