Geomorphology 305 (2018) 94–111

Contents lists available at ScienceDirect

Geomorphology

journal homepage: www.elsevier.com/locate/geomorph

Niche construction within riparian corridors. Part I: Exploring biogeomorphic feedback windows of three pioneer riparian species (Allier River, France)

Borbála Hortobágyi [a,b,*], Dov Corenblit [a,b], Johannes Steiger [a,b], Jean-Luc Peiry [a,b,1]

[a] Université Clermont Auvergne, CNRS, GEOLAB, F-63000 Clermont-Ferrand, France
[b] LTER France, LTSER Zone Atelier Loire, F-37000 Tours, France

ARTICLE INFO

Article history:
Received 16 December 2016
Received in revised form 23 August 2017
Accepted 23 August 2017
Available online 31 August 2017

Keywords:
Establishment area
Biogeomorphic feedback window
Longitudinal and transverse gradients of alluvial bars
Riparian *Salicaceae* species

ABSTRACT

Within riparian corridors, biotic-abiotic feedback mechanisms occur between woody vegetation strongly influenced by hydrogeomorphic constraints (e.g., sediment transport and deposition, shear stress, hydrological variability), fluvial landforms, and morphodynamics, which in turn are modulated by the established vegetation. During field investigations in spring 2015, we studied 16 alluvial bars (e.g., point and lateral bars) within the dynamic riparian corridor of the Allier River (France) to assess the aptitude of three pioneer riparian *Salicaceae* species (*Populus nigra* L., *Salix purpurea* L., and *Salix alba* L.) to establish and act as ecosystem engineers by trapping sediment and constructing fluvial landforms. Our aim is to empirically identify the preferential *establishment area* (EA; i.e., the local areas where species become established) and the preferential *biogeomorphic feedback window* (BFW; i.e., where and to what extent the species and geomorphology interact) of these three species on alluvial bars within a 20-km-long river reach. Our results show that the EA and BFW of all three species vary significantly along the longitudinal profile, i.e., upstream-downstream exposure on the alluvial bars, as well as transversally, i.e., the main hydrological connectivity gradient from the river channel toward the floodplain. In the present-day context of the Allier River, *P. nigra* is the most abundant species, appearing to act as the main engineer species affecting landform dynamics at the bar scale; *S. purpurea* is established and acts as an ecosystem engineer at locations on alluvial bars that are most exposed to hydrosedimentary flow dynamics, while *S. alba* is established on the bar tail close to secondary channels and affects the geomorphology in mixed patches along with *P. nigra*. Our study highlights the role of functional trait diversity of riparian engineer species in controlling the extent of fluvial landform construction along geomorphic gradients within riparian corridors exposed to frequent hydrogeomorphic disturbances.

1. Introduction

On alluvial bars of high-energy river reaches, interactions occur between pioneer riparian woody vegetation and hydrogeomorphic processes (Gurnell, 2014). Hydrogeomorphic conditions (sediment texture, exposure to shear stress, topographic level, and hydrological variability) exert a strong influence on vegetation dynamics, and in turn, the established vegetation can modulate the water flow as well as the sediment, landform geomorphology, and topography (Gurnell et al., 2005; Corenblit et al., 2007; Bertoldi et al., 2011). These reciprocal interactions lead to strong feedbacks between fluvial landforms and riparian vegetation during the early stages of vegetation succession.

A significant literature on biogeomorphic topics has emerged over the last 20 years in an attempt to develop conceptual models to explain feedbacks between fluvial geomorphology and riparian vegetation dynamics. In ecology, the concepts of *ecosystem engineer* (Jones et al., 1994) at the community level and *niche construction* (Odling-Smee et al., 2003) at the population level have been applied in the riparian context where certain engineer plant species appear to control riparian ecosystem structure and function by significantly modifying hydrogeomorphic processes, landforms and fluvial habitats (Edwards et al., 1999; Gurnell and Petts, 2006; Corenblit et al., 2007, 2011, 2014; Gurnell, 2014). Such dynamic ecosystems, which are subject to frequent physical disturbances (e.g., floods in rivers) and exhibiting ecological and potentially ecoevolutionary feedbacks between geomorphology and engineer plants, have been defined as *biogeomorphic ecosystems* (Balke et al., 2014; Corenblit et al., 2015). Within biogeomorphic ecosystems, the synergetic construction of fluvial landforms, the vegetation succession, and the life cycle of riparian trees have been described (i) within the ecosystem engineer framework as a *biogeomorphic succession* (Corenblit et al., 2007) and (ii) within the niche construction framework as a *biogeomorphic life cycle* (Corenblit et al., 2014).

In the initial stages of the biogeomorphic succession and biogeomorphic life cycle, successful colonization by riparian *Salicaceae*

---

[*] Corresponding author at: Université Clermont Auvergne, CNRS, GEOLAB, F-63000 Clermont-Ferrand, France.

E-mail address: borbala.hortobagyi@uca.fr (B. Hortobágyi).

[1] Present address: CNRS, UMI3189, "Environnement, Santé, Sociétés", Faculté de Médecine, UCAD, BP 5005, Dakar-Fann, Senegal.

http://dx.doi.org/10.1016/j.geomorph.2017.08.048

species (RSS) depends on the relations between the hydrogeomorphic disturbance regime, initial habitat conditions, seed dispersal, and seedling recruitment dynamics (Mahoney and Rood, 1998; Perona et al., 2012; Balke et al., 2014). Mahoney and Rood (1998) initially proposed a vegetation recruitment model (*recruitment box model*) based on four key parameters of recruitment: (i) flow variability; (ii) period of seed dispersal; (iii) rate of stream stage decline; and (iv) elevation above the low stream stage. Balke et al. (2011, 2014) defined the concept of *Window of Opportunity* (WoO) in a biogeomorphic ecosystem as a 'sequence of a disturbance-free period of sufficient length for seedling anchorage following a dispersal event'. In the field, we identify the *establishment area* (EA) within a disturbance-driven biogeomorphic ecosystem as the geographic area where vegetation is actually established following a WoO. Once ecosystem engineer species exceed the establishment threshold, a critical engineering threshold must also be exceeded to allow biogeomorphic feedbacks to occur (Corenblit et al., 2007). The concept of a *biogeomorphic feedback window* (BFW), as proposed by Eichel et al. (2015) for high mountain environments, provides a suitable framework for identifying the occurrence of spatiotemporal feedbacks between geomorphic and vegetation dynamics. These authors (*op. cit.*) successfully used ordination (nonmetric multidimensional scaling) and post hoc correlation methods to analyse the relation between engineer plant species and geomorphic processes and identified the optimal conditions for the occurrence of biogeomorphic feedbacks between specific plant assemblages and hillslope processes leading to the development of solifluction lobes. In the case of fluvial environments, we define BFW as a specific spatiotemporal envelope of interactions taking place between hydrogeomorphic and RSS dynamics (e.g., *Populus nigra* L., *Salix purpurea* L., and *Salix alba* L.) that trigger strong biogeomorphic feedbacks.

In our study, we investigate the spatial extent of this BFW, i.e., the geographic areas within the riparian corridor where RSS can act as ecosystem engineers. The resistance and resilience of biogeomorphic ecosystems are intimately linked to the BFWs of engineer plants (Corenblit et al., 2015). In the ecological literature, mainly two forms of resilience are distinguished: (i) ecological resilience sensu Holling (1973) corresponds to the ability of a system to retain essential processes when disturbed while maintaining its structural and functional integrity before changing to another domain of attraction, i.e., it can be measured as the magnitude of disturbance that the system can tolerate and still persist (Holling, 1973; Carpenter et al., 2001); and (ii) engineering resilience, which is a more traditional view, representing the ability of a system to resist physical disturbance; it can be measured as the rate at which the system returns to equilibrium following a disturbance (Pimm, 1984; Carpenter et al., 2001; Gunderson et al., 2010). We use resilience here in the sense of ecological resilience and resistance in the sense of engineering resilience. The latter reflects the physical resistance of plants and fluvial landforms to mechanical constraints during hydrogeomorphological disturbances (floods). Vegetation can establish and resist hydrogeomorphic constraints to a certain point and thus generate feedbacks by modifying the hydrogeomorphic environment. As a result, vegetation will influence the resistance of landforms to hydrogeomorphic disturbances and enhance their recovery after destructive-dominated flood events, therefore also affecting the persistence of biogeomorphic landforms, i.e., ecological resilience.

By filtering morphological, biomechanical, phenological, and physiological traits, hydrogeomorphic processes control species composition on alluvial bars in the early stages of succession (Richter and Richter, 2000). Few woody riparian species develop traits adapted to the highly disturbed riparian environments where shear stress, erosion, sediment burial, and drought make it difficult for plants to establish (Gurnell, 2014). The RSS such as poplars and willows are recognized as the main species capable of (i) establishing on exposed alluvial bars and (ii) potentially affecting the geomorphology. Such species have developed particular traits in response to hydrogeomorphic disturbances, adapting their reproduction (sexual and asexual modalities), as well as their morphological and biomechanical properties to fluvial environments (Karrenberg et al., 2002; Lytle and Poff, 2004). A significant body of research has identified several riparian engineer species belonging to the *Salicaceae* (Gurnell, 2014), including, for example, *Populus nigra* L., which is widely distributed within the European continent (Gurnell and Petts, 2006).

However, to our knowledge, the distinction between RSS concerning their specific affinity to establish on alluvial bars and their effect on geomorphology has been given little consideration. The RSS exhibit large variations in their physiological, morphological, and biomechanical functional attributes and thus (i) they may colonize different areas with contrasted habitat conditions on alluvial bars (Johnson, 2000; Guilloy-Froget et al., 2002; Pasquale et al., 2013), and (ii) they potentially affect geomorphology differently because they are not distributed over the same range of exposure to hydrogeomorphic constraints and display different morphologies and biomechanical attributes at the interspecific level, but also at the intraspecific level in relation with environmental conditions (Hortobágyi et al., in press). Based on these considerations, we hypothesize that RSS act differently as ecosystem engineers within a given river reach and that their effects on geomorphology vary in intensity according to their location along (i) the upstream-downstream gradient of exposure on alluvial bars; (ii) the transverse gradient of connectivity from the main channel toward the floodplain; and (iii) to their physiognomic attributes such as stem height, diameter, and density.

We focus on the biogeomorphic succession or the biogeomorphic life cycle of RSS (Corenblit et al., 2007, 2014), from the end of the pioneer phase (1 year) to the end of the biogeomorphic phase (10 years) before entering into the ecological phase. At the beginning of the pioneer phase (after germination and during the beginning of the growth season, corresponding to the first 6 months), RSS seedlings may exert a surface protection and stabilizing effect when grouped in dense aggregates. However, these seedlings are not yet able to have a strong effect on hydrogeomorphic processes and fluvial landforms. If RSS seedlings resist drought during the summer (first 6 months) and then floods during the autumn-winter period (second 6 months), they start to be potentially capable of affecting hydrogeomorphic processes. The ecological phase can be determined by multiple criteria, e.g., taxonomic and topographic (Corenblit et al., 2009) or pedologic (Bätz et al., 2015). We determine here the onset of the ecological phase as the moment when *P. nigra* (the most abundant species in our study area) finishes constructing its optimal habitat and reaches sexual maturity (see part 2 this issue; Corenblit et al., accepted). Under optimal conditions, this time lapse is 10 years on average (Isebrands and Richardson, 2014), but may be delayed or even impeded when the vegetation is exposed to very high-energy hydrogeomorphic conditions or in the case of channelized and regulated rivers. During the ecological phase, vegetation is rather disconnected from annual floods and sediment fluxes, and their interactions with hydrogeomorphic processes are weak (Corenblit et al., 2009). Conversely, the biogeomorphic phase is characterized by the possibility of strong interactions between vegetation and hydrogeomorphic processes. Under specific spatiotemporal conditions, a *biogeomorphic feedback window* (BFW) may open and lead to biogeomorphic feedbacks during this critical phase of riparian ecosystem organization. We focus here on the three most abundant ligneous RSS: *Populus nigra* L., *Salix purpurea* L., and *Salix alba* L., found on the alluvial bars of a dynamic reach of the Allier River, France. The hypothesis tested here is that the occurrence and location of the EA and BFW are likely to vary for these three species, depending on their distribution on the alluvial bars along the upstream-downstream (longitudinal) exposure gradient and main channel-floodplain (transverse) gradient of connectivity. In this empirical study, the main objectives are as follows:

1. to determine the EA of *P. nigra*, *S. purpurea*, and *S. alba* on alluvial bars along the upstream-downstream exposure gradient and the transverse gradient of connectivity from the main channel toward the floodplain;

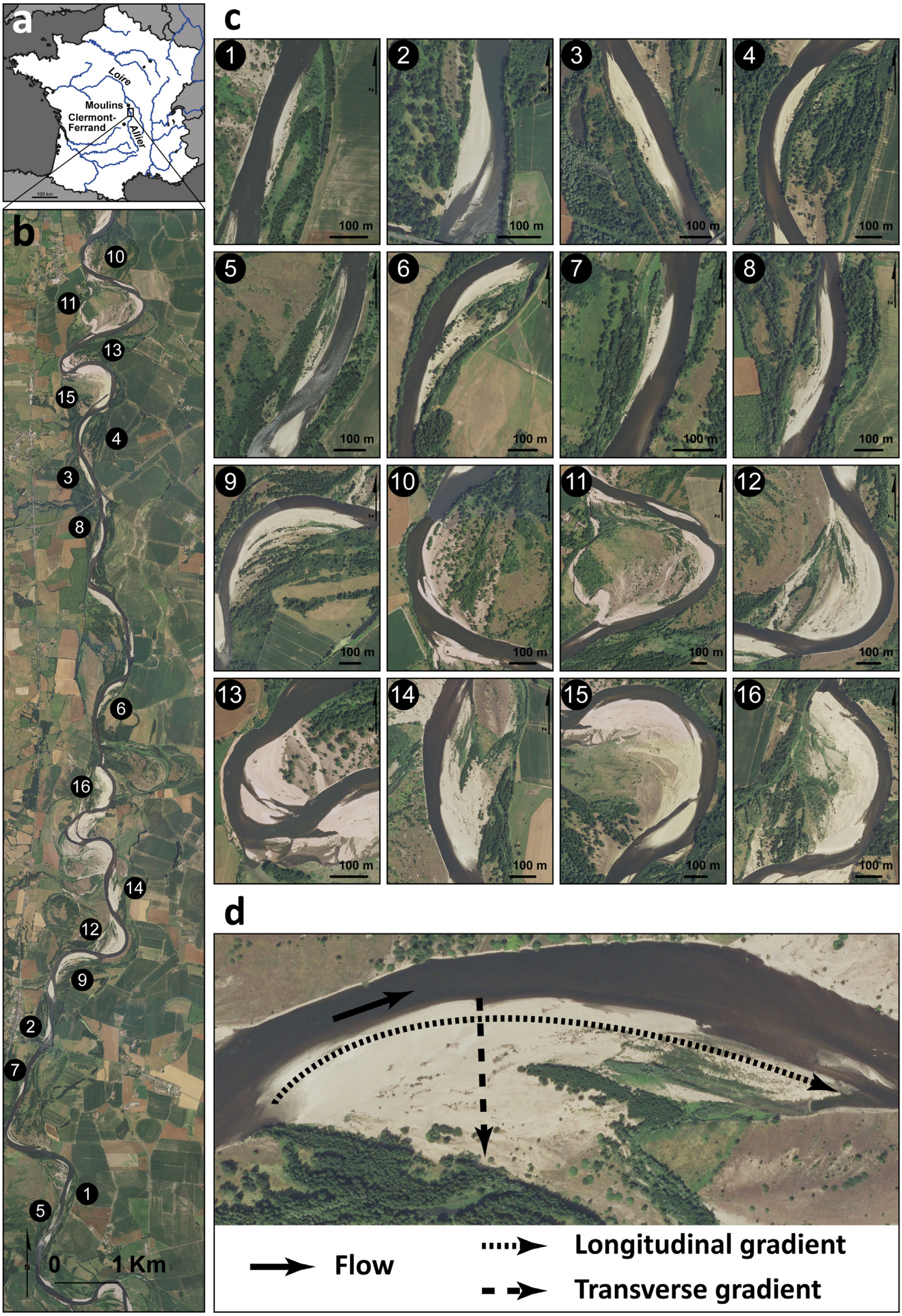

Fig. 1. The study reach of the Allier River and the 16 alluvial bars ranked from 1 to 16 according to increasing lateral erosion rate (1.45, 1.61, 1.74, 1.78, 1.93, 2.01, 3.13, 4.37, 5.26, 5.57, 7.59, 7.61, 8.65, 10.10, 16.49 $m^2/m/year$) calculated from aerial photographs taken in 2005 and 2013.

2. to ascertain whether the three species act as ecosystem engineers, i.e., the existence of a biogeomorphic feedback window (BFW) for each species, which leads to significant biogeomorphic feedbacks; and
3. if point 2 proves to be the case, to determine the specific BFW of each species.

2. Methods

2.1. Study reach

The study reach is located in the lower Allier River (France), which is a dynamic wandering/meandering gravel bed river (Fig. 1). A 20 km reach was chosen between the Sioule River confluence and Moulins. This reach is characterized by active lateral erosion on the outer bends of meanders, with point bar formation and migration on the inner bends within the *Réserve Naturelle Nationale du Val d'Allier*. The area benefits from a certain protection status and has experienced moderate anthropogenic impacts (e.g., few bank protections or rip rap) (Petit, 2006; Dejaifve and Esquirol, 2011). The erosion rate between 2005 and 2013 calculated for each alluvial bar varies between 1.54 and 16.49 m^2/m/y (Fig. 1).

2.2. Life history of *Populus nigra*, *Salix purpurea* and *Salix alba*

We focus on three pioneer woody riparian plant species belonging to the *Salicaceae* family, *Populus nigra*, *Salix purpurea*, and *Salix alba*, which are widely distributed in high-energy river reaches in Europe and which are dominant on the alluvial bars of the Allier River. All three species potentially act as ecosystem engineers but in different ways according to their specific physiognomic attributes, location on the alluvial bars, and abundance (Table 1). In terms of water access, *P. nigra*, *S. purpurea*, and *S. alba* are all mesohygrophilic species. However, *S. alba* requires a high and stable water table (Isebrands and Richardson, 2014; Houston Durrant et al., 2016). *Populus nigra* seedlings are considered to be more resistant to drought than *S. alba* (Splunder et al., 1996). A comparative study of *S. alba* and *S. purpurea* reveals better drought resistance of the latter species (Lavaine, 2013). This plant species produces less biomass, showing less reduction in structural root production (roots with a diameter up to 5 mm) and a high shoot-to-root ratio under conditions of stress. In the absence of induced drought stress, *S. purpurea* shows a very high aboveground biomass production (more marked than belowground) but a lower growth rate than *S. alba*. *Salix purpurea* is also a stress-tolerant species in relation to extreme heat, drought, and long periods of submersion (Isebrands and Richardson, 2014), and thus it is well adapted to become established on gravel bars. *Populus nigra* also colonizes exposed moist sandy alluvial surfaces, which provide the optimum seedbed following seasonal flooding (Isebrands and Richardson, 2014). The species has a good capacity of adaptation to flood-induced constraints such as prolonged submersion, mechanical stress, droughts, or sediment burial, as it has a high phenotypic plasticity. The physiological, morphological (size and shape), and biomechanical (flexibility) properties make *P. nigra* well adapted to this unstable and heterogeneous environment (Corenblit et al., 2014). For a detailed description of the life cycle of *P. nigra*, see Corenblit et al. (2014).

2.3. Field sampling and GIS

A total of 126 vegetation patches were sampled on the 16 alluvial bars. Patches are composed of one of the species *P. nigra*, *S. purpurea*, or *S. alba* or a mixture in varying proportions, with or without the presence of a herbaceous mat. Vegetation height within all sampled patches is <3 m, and all patches are highly connected to hydrogeomorphic processes as they are located on the alluvial bar at a relatively low elevation near the water level. Sampling was undertaken in April 2015 during low water stage when the youngest patches were not submerged. Furthermore, the absence of leaves during this period facilitates the estimation of abiotic and biotic parameters (i.e., biogeomorphic accumulation landforms, stem diameter, density, and vegetation degradation degree). The

Table 1
Ecological summary of *Populus nigra* L., *Salix purpurea* L., and *Salix alba* L. (Karrenberg et al., 2002; Rameau et al., 2008; Lavaine, 2013; Isebrands and Richardson, 2014).

Parameters		*Populus nigra* L.		*Salix purpurea* L.		*Salix alba* L.	
Morphotype		Tree, reaching heights of 40 m and diameters over 2 m at maturity		Shrub, medium-sized to tall shrub or small tree can grow up to 4 m but usually 1–2 m tall, branches of 0.6–1.5 cm diameter		Tree, attaining heights of 30 m and trunks up to 1 m or more in diameter	
Reproduction		Sexual and vegetative					
Seed dispersal		Large quantities (poplars can produce 30–50 million seeds in a single season) of tiny seeds attached to a cottony coma dispersed by wind (anemochory) or water (hydrochory)					
Seed longevity		20 days		*Salix*: limited longevity			
Recruitment conditions depends on:		Water level in the channel, the groundwater table, sediment texture, availability of bare sediment					
Longevity		Up to 400 years		>50 years		5–50 years	
Growth rate		High: within their first growing season up to a height of 0.5–1 m, rapid root expansion					
Root system		Poplars: downwardly directed 'sinker' roots and horizontal roots and can develop root suckers		Salix species: one main downwardly oriented taproot, which thickens with age			
Autecology	Light	Heliophilous		Heliophilous		Heliophilous	
	Edaphic condition	pH from basic to neutral Coarse alluvial material (sand, gravel, silt), aerated soil Mesohygrophilic, slightly hygrophilic in regularly flooded environment		pH neutral Frequently coarse alluvial material (clay, gravel, sand) Mesohygrophilic to mesophilic, on annually flooded soil, occasionally mesoxerophilous when behaving as a pioneer		pH from basic to neutral Alluvial material (clay-silt, sand, gravel or pebble well aerated) Mesohygrophilic	
		*	**	*	**	*	**
*Ecological valence (Julve, 2016) and **Ellenberg indicator values (Evette et al., 2012)	Light	8	5	8	8	8	5
	Moisture	7	8	8	x	8	8
	Reaction	7	7	7	8	7	8
	Nutrient	7	7	5	x	7	7
	Organic matter	8		1		8	

Light: 1 – shade, 9 – light; Moisture: 1 – dry, 12 – humid; Reaction: 1 – acidic, 9 – alkaline; Nutrient: 1 – poor, 9 – rich; Organic matter: 1 – poor, 9 – rich, x = species indifferent to all categories.

patch survey includes assessment of the following parameters: geomorphic (main geomorphic process, patch, and alluvium grain size), ecological (species abundance, stem density and diameter, vegetation height and occurrence of a herbaceous mat within the patch), morphometric (ease of delimitation of patches, degree of degradation, and tilting of the vegetation), and biogeomorphic (occurrence of biogeomorphic accumulation landforms and presence of sediment tail on the leeside of the patch). All parameters are visually assessed in the field using categorical groups. The main geomorphic processes are clearly erosion dominated, clearly deposition dominated, or are neither erosion or deposition dominated. The dominant sediment size is assessed as sand, gravel, or coarse gravel. Species abundance is expressed as the percentage of the three species (*P. nigra*, *S. purpurea*, and *S. alba*) within a patch, giving a total of 100%. For stem density, the three categories used are based on the distance between stems, i.e., low (>1 m), medium (0.5–1 m), and high (<0.5 m). Four categories are created for stem diameter: very small (<1 cm), small (1–2 cm), medium (2–4 cm), and large (>4 cm). Vegetation height is determined for each of the three species within each patch, then weighted by the abundance of species to calculate the average weighted height of the patch. The average is divided into four categories: very small (<0.5 m), small (0.5–1 m), medium (1–1.5 m), and tall (>1.5 m). The occurrence of a herbaceous mat within the patch is estimated as none, very low, high, or very high. The ease of delimitation of patches is also assessed by a visual estimation such as low, medium, or high, as well as the degree of degradation and tilting of the vegetation that are categorized as none, low, or high. The degradation of the vegetation relates to the damage caused by impacts during floods, involving coarse sediment or dead wood, and the resulting broken stems or branches and signs of impact on the stem. The presence or absence of biogeomorphic accumulation landforms is also noted; one of the types of accumulation features is the sediment tail on the leeside of the patch. All patches are localized using a GPS (Trimble GeoXH).

Field data are supplemented with variables calculated in a GIS (e.g., distance from channel, position on the alluvial bar, and minimum age). The fieldwork took place over several days, and the water level was variable during sampling. Therefore, the determination of the distances of the patches from the channel (transverse gradient: close, middle, far) is based on the aerial photographs of 2013 to ensure a constant water line. The aerial photographs were taken between 11 and 14 July 2013 when flow conditions were very similar to those during field sampling. The position of patches along the longitudinal gradient (upstream, central, and downstream) on the alluvial bar is calculated by dividing the alluvial bar into three parts along the water line. The limits of the classes for the transverse gradient are calculated by subtracting or adding the standard deviation from the mean value. The minimum age is considered as an approximate age estimation for the patch based on three aerial photographs (2009 – resolution of 0.30 m, 2011 – resolution of 0.30 m and 2013 – resolution of 0.25 m). This method does not give the exact age because very young or small patches cannot be detected on aerial photographs, and aerial photographs are not available for every year. However, this variable gives an estimation of the duration of existence of the patch with an error of between 1 and 3 years.

2.4. Data analysis

First, we use descriptive statistics and statistical tests to see how longitudinal and transverse gradients control biotic and abiotic variables and which variables are conditioning the occurrence of the biogeomorphic feedback windows of each of the three species on alluvial bars. For qualitative variables, we use contingency tables and a X^2 test of independence along with Fisher's exact probability test. This test determines if the difference with the theoretical value is significant or not; for each cell, the test indicates if the actual value is equal (=), lower (<), or higher (>) than the theoretical value. For quantitative variables, the Kruskal-Wallis nonparametric test is applied with a Steel-Dwass-Critchlow-Fligner multiple pairwise comparison procedure to identify which samples are responsible for rejecting H_0. Letters are assigned to groups (i.e., A, B) indicating that the groups are significantly different.

In a second step, we use an ordination technique (nonmetric multidimensional scaling, NMDS) with post hoc correlation as proposed by Eichel et al. (2015) to assess the relationships between biotic and abiotic variables and geomorphic characteristics. The NMDS is a rank-order-based method that represents as well as possible the ordering relationships among objects (their proximity indicates similarity) along a predetermined small number of axes. Ordinations of objects can be produced from any distance matrix with the ordination axes indicating the main variation (gradient) of the variables. Except for the distance used for NMDS, see Eichel et al. (2015) for a description of the method and for details about the ordination technique. After a comparison of dissimilarity indices for the detection of gradients, the Gower distance appears to be the most appropriate for our dataset. We use nonmetric multidimensional scaling ordination to assess which abiotic factors (position on longitudinal and transverse gradient) influence the species composition, biogeomorphic landforms, and other biotic factors of the patches.

Logistic regression modelling (Logit) is used to predict the probability of occurrence of a given species or biogeomorphic accumulation landform according to the longitudinal and transverse gradients.

The descriptive statistics and statistical tests are carried out within XLSTAT software, while the NMDS is performed with the statistical computing software R (R Core Team, 2015) using metaMDS in the R vegan package (Oksanen et al., 2016). We use Envfit (R vegan) for post hoc correlation. Logit models are also computed in R software.

3. Results

3.1. Longitudinal and transverse gradients: sediment and vegetation

Most of the abiotic and biotic parameters on the alluvial bars respond significantly to the longitudinal (upstream–downstream) or transverse (main channel to floodplain) gradients, or both (Table 2). Regarding the longitudinal gradient, significant differences between patches almost exclusively concern up- and downstream locations, i.e., bar heads and tails. Bar heads display a coarse sediment matrix, whereas the matrix of the central and downstream locations is dominated by sand. Patches older than two-years are positively associated with downstream locations, whereas one-year old patches are mainly found on bar heads where vegetation is of very small height (mean ± SD: 0.82 ± 0.69 m) with very small stem diameter (1.35 ± 1.37 cm). Seventy percent the patches at upstream locations and 79% of the patches close to the main channel are highly damaged, and no herbaceous vegetation cover is present within these patches. In contrast, patches at downstream locations are characterized by the tallest vegetation size classes on the alluvial bars and also the largest diameters (respectively 1.19 ± 0.57 m and 1.68 ± 0.81 cm) and highest stem densities (stem spacing < 1 m). These patches are generally (in 77% of the cases) covered by a dense herbaceous mat. Conversely to the longitudinal gradient, the sediment matrix is not structured along the transverse gradient. However, riparian trees are younger and smaller, with smaller stem diameters close to the main channel (0.56 ± 0.33 cm) than close to the floodplain (0.97 ± 0.62 cm). Similarly to upstream locations, the riparian trees are highly damaged and no herbaceous vegetation cover occurs within the patches close to the main channel. By contrast, riparian trees in the middle location of the bar or close to the floodplain are older and taller (middle location: 1.04 ± 0.71 m, far: 1.31 ± 0.84 m) with larger stem diameter (middle location: 1.52 ± 1.23 cm, far: 2.02 ± 1.56 cm) than trees close to the main channel. These trees are rarely damaged by flood flow, and a dense herbaceous vegetation cover is present.

Table 2
Biotic and abiotic parameters along the longitudinal and transverse gradients: the *p*-values of X^2 and pairwise test results (> attraction, < repulsion from the variable) are indicated in grey when significant.

Parameters		Longitudinal gradient			Transverse gradient		
		Upstream	Central	Downstream	Close	Middle	Far
Sediment grain size at the bar surface	Sand	**<**	**<**	**>**	>	>	<
	Gravel	<	>	<	>	<	<
	Coarse gravel	**>**	>	**<**	<	>	>
p-value at α = 0.05			**<0.0001**			0.26	
Vegetation age	1	>	>	**<**	>	<	>
	2	**<**	<	**>**	>	<	<
	4	<	>	<	<	>	>
	6	>	<	<	**<**	**>**	<
p-value at α = 0.05			**0.008**			**0.08**	
Vegetation height	Very small	**>**	>	**<**	>	<	<
	Small	<	<	>	**>**	**<**	**<**
	Medium	<	<	>	>	<	>
	Tall	<	>	>	**<**	>	>
p-value at α = 0.05			**0.007**			**0.0003**	
Stem diameter	Very small	**>**	>	**<**	>	<	<
	Small	<	<	**>**	>	<	>
	Medium	**<**	>	>	**<**	>	>
	Big	>	>	**<**	**<**	>	>
p-value at α = 0.05			**0.003**			0.19	
Stem density	Low	>	>	**<**	<	>	<
	Medium	<	<	>	<	<	>
	High	<	<	>	>	>	**<**
p-value at α = 0.05			**0.03**			0.18	
Degree of vegetation degradation through flood damage	None	**<**	>	>	**<**	>	**>**
	Low	>	<	<	>	>	**<**
	Strong	**>**	<	<	**>**	**<**	<
p-value at α = 0.05			**0.008**			**0.0002**	
Occurrence of herbaceous mat	None or very low	**>**	>	**<**	**>**	<	**<**
	(Very) high	**<**	<	**>**	**<**	>	**>**
p-value at α = 0.05			**0.001**			**0.0005**	

3.2. RSS patches: *P. nigra*, *S. purpurea* and *S. alba*

The three pioneer riparian ligneous species (i.e., *P. nigra*, *S. purpurea*, and *S. alba*) are unequally represented in our study area in terms of abundance. Out of the total number of 126 sampled patches on the 16 alluvial bars, *P. nigra* occurs in 101 patches, *S. purpurea* in 55, and *S. alba* in 26 (Table 3). In terms of average abundance, *P. nigra* again is the dominant species, making up >65% of the total abundance for the three

Table 3
Presence of the three species and comparison of their abundance within vegetation patches according to the longitudinal and transverse gradients (PN = *P. nigra*, SP = *S. purpurea*, SA = *S. alba*; SD = standard deviation; letters are assigned to groups (i.e., A, B) indicating that the groups are significantly different, significant differences are indicated in bold).

Species	Parameters	Longitudinal gradient			Transverse gradient			Abundance of patches	Average abundance (%)
		Upstream	Central	Downstream	Close	Middle	Far		
PN	N	32	37	32	12	66	23	101	
	%	25.40	29.37	25.40	9.52	52.38	18.25	80.16	
	Mean (%)	58.51	74.93	65.71	31.25	74.73	80.92		66.25
	SD	45.32	41.69	36.81	42.9	37.05	34.11		
	Group	**A**	**B**	**AB**	**A**	**B**	**B**		
	p-value at α = 0.05	**0.04**			<**0.0001**				
SP	N	25	12	18	23	24	8	55	
	%	19.84	9.52	14.29	18.25	19.05	6.35	43.65	
	Mean (%)	34.04	18.75	20.29	65.36	12.84	14.79		24.88
	SD	43.67	37.48	27.41	44.45	25.38	29.94		
	Group	**A**	**B**	**AB**	**A**	**B**	**B**		
	p-value at α = 0.05	**0.05**			<**0.0001**				
SA	N	6	6	14	3	21	2	26	
	%	4.76	4.76	11.11	2.38	16.67	1.59	20.63	
	Mean (%)	7.45	6.32	14	3.39	12.43	4.29		8.87
	SD	24.74	22.41	24.34	12.48	27.58	19.99		
	Group	**A**	**A**	**B**	A	A	A		
	p-value at α = 0.05	**0.01**			0.04				
Total number of patches	N	47	44	35	38	111	33	126	
	%	37.30	34.92	27.78	20.88	60.99	18.13	100	

Table 4
Presence of monospecific and mixed species patches according to the longitudinal and transverse gradients (PN = *P. nigra*, SP = *S. purpurea*, SA = *S. alba*; the *p*-values of X^2 and pairwise test results (> attraction, < repulsion from the variable) are indicated in grey when significant).

Species		Longitudinal gradient						Transverse gradient						Abundance of monospecific and mixed patches
		Upstream		Central		Downstream		Close		Middle		Far		
PN	N	18	<	29	>	12	<	5	<	40	>	14	>	59
	%	14.29		23.02		9.52		3.97		31.75		11.11		46.8
SP	N	13	>	6	<	1	<	16	>	3	<	1	<	20
	%	10.32		4.76		0.79		12.70		2.38		0.79		15.9
SA	N	2	>	1	<	1	<	0	<	4	>	0	<	4
	%	1.59		0.79		0.79		0.00		3.17		0.00		3.2
MIX	N	14	<	8	<	21	>	7	<	27	>	9	>	43
	%	11.11		6.35		16.67		5.56		21.43		7.14		34.1
p-value at α = 0.05				0.0005						<0.0001				
Sum (PN+SP+SA+MIX)	N	47		44		35		28		74		24		126
	%	37.30		34.92		27.78		22.22		58.73		19.05		100

species; *S. purpurea* accounts for 25%, and finally, *S. alba* for <10% of the average abundance (Table 3). On monospecific patches, *P. nigra* remains dominant, with a total of 59 monospecific patches among the 126 patches; *S. purpurea* accounts for 20 patches and finally, *S. alba* for only 4 patches. The three species coexist on 43 patches (Table 4).

The first NMDS axis is mainly related to the variable that indicates the position on the upstream-downstream profile (Longitudinal; $r^2 = 0.20$); this axis is mostly linked to the longitudinal gradient of energy which classically decreases from bar head to bar tail. However, this variable is also related to the transverse gradient. The second NMDS axis is mainly related to the variable indicating the distance from the main channel (Transverse; $r^2 = 0.26$); and is linked to the transverse gradient of exposure. Four patch types can be identified based on the NMDS results (Fig. 2A). Fig. 2B shows a schematic representation of the four patch types. Type 1: small *P. nigra* monospecific patches with small diameters and low stem densities found upstream and in central bar locations on the longitudinal gradient and mainly at middle locations away from the main channel in coarse sediment. Type 2: the second group is mainly composed of monospecific patches of *S. purpurea*, which are also small and characterized by small stem diameters. These patches are composed of strongly tilted, flood-damaged riparian vegetation located at upstream or central locations of the alluvial bars, close to the channel in coarse sediment where erosive processes dominate. Type 3: these patches are mainly composed of *P. nigra* and *S. purpurea* at variable locations on the two gradients: the vegetation being taller, older, and damaged by floods and having larger stem diameters and higher stem density. Type 4: older patches composed exclusively of *P. nigra* or a combination of *S. alba* and *P. nigra* of large size and stem diameter, being located mostly downstream or at middle or far locations away from the channel in fine sediment. Dense herbaceous mats and intact patches mostly occur within this type of patch. While *P. nigra* and *S. purpurea* are discriminated by the second axis, they nevertheless occur together mostly at downstream locations or within older patches (influence of the first axis). *Salix alba* is discriminated from the two other species on the first axis.

The estimated minimum age is clearly discriminated on the first NMDS axis, with the youngest patches plotting on the left side of the axis, 2- and 4-year-old patches in the central location, and the oldest patches found on the right-hand side (Fig. 3). The youngest patches, mainly composed of monospecific *P. nigra*, are located at upstream or central locations on the longitudinal gradient and on all three locations of the transverse gradient. Numerous 2-year-old patches are located downstream, but *S. purpurea* is exclusively present on patches located at upstream or central locations on the longitudinal gradient, or close to the main channel. The 6-year-old riparian tree patches are located at medium location with respect to the distance of the channel.

3.3. Establishment area of the three species

The number of patches is unequally distributed along the longitudinal gradients of the alluvial bars. We observe 47 patches upstream, 44 at central locations, and 35 downstream (Table 3). The presence of species within patches also varies along this gradient. Significant difference has been found in the relative abundance of all three species between the three locations (Table 3). *Populus nigra* occurs preferentially in the central location of the alluvial bars and is the less present upstream. *Salix purpurea* occurs mostly upstream and is present less at the central location. The downstream location is not significantly different from upstream and central locations for both species as regards species occurrence. *Salix alba*, on the contrary, is the most abundant species at the downstream location, and its proportion remains low at the upstream and central locations. Monospecific *P. nigra* patches are more developed at the central location of the alluvial bars, and monospecific *S. purpurea* patches are found upstream. None of the species belonging to the monospecific patches are positively associated with the downstream location (Table 4). Only four *S. alba* monospecific patches are observed out of the total of 126. The presence of mixed species patches is positively associated with the downstream but not with the central location.

The number of patches is unequally distributed also along the transverse gradient: 38 patches are located close to the main channel, 111 at middle distance, and 33 far from the channel (Table 3). The presence of species within patches also varies along the transverse gradient. The abundance of *P. nigra* is higher far from the channel. Conversely, *S. purpurea* shows the highest abundance close to the channel (Table 3). The pairwise comparison procedure does not reveal significant differences in the case of *S. alba* abundance. The presence of monospecific *P. nigra* patches is more apparent farther away from the channel, in contrast to *S. purpurea* (Table 4). The four *S. alba* monospecific patches are observed at the middle location. The presence of mixed species patches is not associated with either of the two gradients.

Logit models show the probability of occurrence of the three species and of monospecific or mixed patches on the longitudinal exposure gradient of alluvial bars (Fig. 4). The probability of occurrence of *P. nigra* and *S. alba* increases along the upstream-downstream gradient, whereas the probability of occurrence of *S. purpurea* slightly decreases along this gradient. Monospecific *P. nigra* patches are present at all locations along the longitudinal gradient, whereas the occurrence of monospecific *S. purpurea* patches strongly decreases downstream. The occurrence of mixed patches composed of two different or all three tree species increases along the upstream-downstream gradient.

Logit models show that the probability of occurrence of the *P. nigra* and *S. purpurea* patches across the transverse gradient varies in an

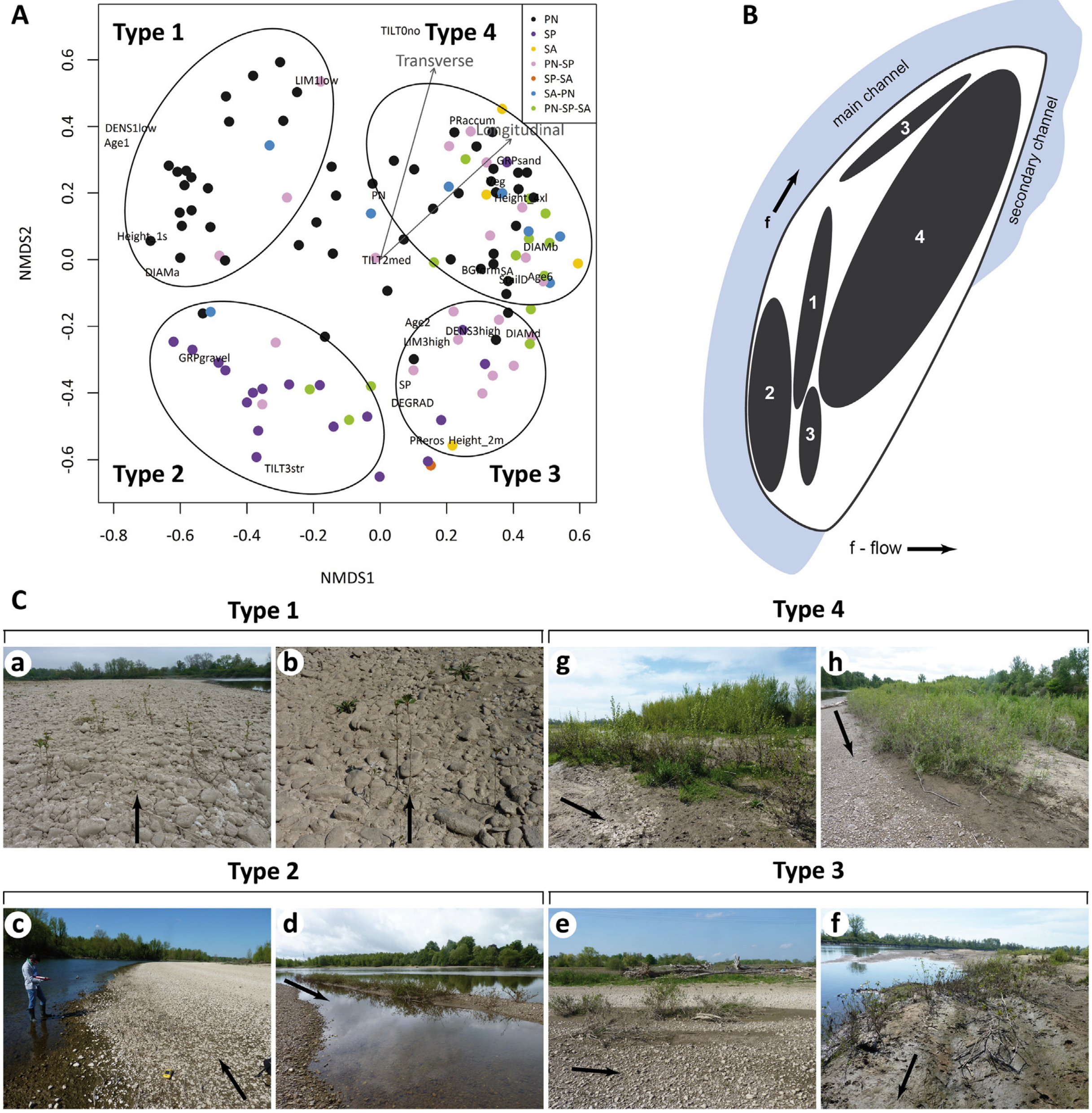

Fig. 2. (A) Ordination results and theoretical location of patch types on the alluvial bar. Results of nonmetric multidimensional scaling (NMDS) superimposed on species composition of patches and environmental fit of significant ($p < 0.01$) variables (arrows). Proximity of patches indicates similar biogeomorphic characteristics, arrows indicate the direction of maximum variable change. Arrow length depends on coefficient of determination (r^2). Three dimensions, stress 0.108. (B) Schematic representation of the four patch types on the alluvial bar. (C) Patch types are illustrated with photographs: (a) and (b) small (young) poplars at highly exposed location without vegetation-induced sediment accumulation; (c) highly exposed *S. purpurea* patch with no biogeomorphic accumulation landform; (d) *S. purpurea* patch with biogeomorphic accumulation landform; (e) less exposed patch composed of *S. purpurea* and *P. nigra*, with biogeomorphic accumulation landforms; (f) patch composed of *S. purpurea* and *P. nigra* at a low-exposure location with biogeomorphic accumulation landforms; (g) poplar patch located downstream with biogeomorphic landform creation and dense herbaceous mat; (h) mixed species downstream location patch with well-developed biogeomorphic accumulation landform.

opposite way in the case of mixed species patches and monospecific patches (Fig. 4). The probability of occurrence of *P. nigra* increases across the transverse gradient of connectivity from the main channel to the floodplain, whereas the probability of occurrence of *S. purpurea* decreases.

We can determine two EAs for each species (Fig. 5b, c, d) based on the NMDS results. The exclusive EA corresponds to the successful establishment of monospecific patches. The extensive EA reflects all habitat conditions where a species can be present, even with a low relative abundance. The exclusive EA of *P. nigra* and *S. purpurea* are entirely separated along the second axis, contrary to *S. alba* whose exclusive EA is superposed onto the exclusive EA of *P. nigra* and the extensive EA of *S. purpurea*. The extensive EA of the three species are superposed on the positive side of the first axis. *Populus nigra* displays the largest extensive EA, with an important overlap with the EAs of the other two species.

The results obtained by natural neighbour interpolation (Fig. 5e, f, g) correspond to the data points presented in Fig. 5b, c, d. However, the interpolation method yields additional information, such as species abundance and a more objective determination of EAs.

3.4. Biogeomorphic feedback window of the three species

Nearly 70% of the sampled patches show visible effects of vegetation on geomorphology, creating biogeomorphic accumulation landforms. Fifty-six percent of the patches where *P. nigra* is present are characterized by vegetation-induced sediment accumulation, compared with

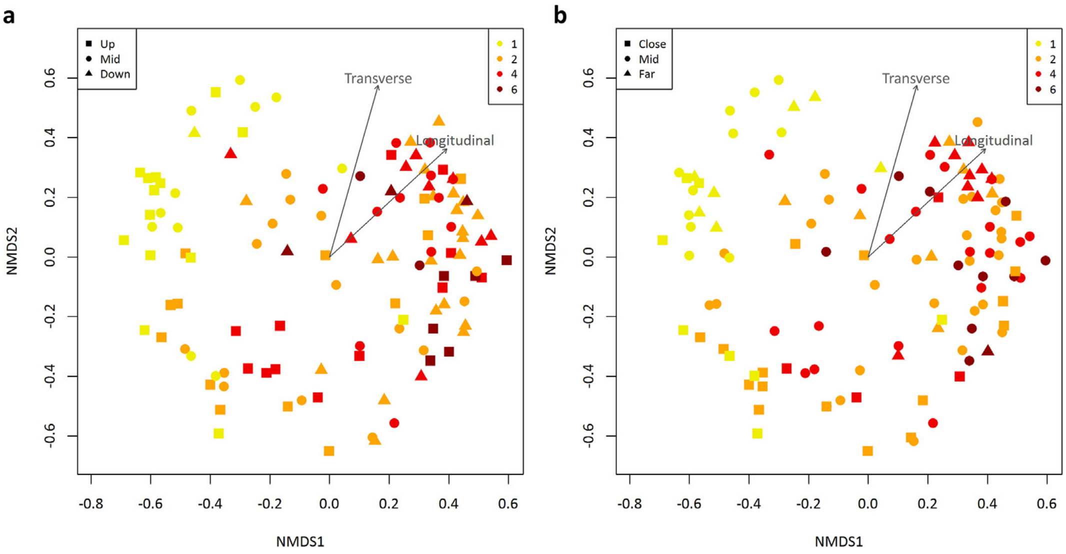

Fig. 3. Results of nonmetric multidimensional scaling (NMDS) superimposed on approximate minimum age of patches and positions along (a) the longitudinal gradient and (b) the transverse gradient and environmental fit of significant ($p < 0.01$) variables (arrows).

35% for *S. purpurea* and 20% for *S. alba* (Table 5). In the presence of biogeomorphic accumulation landforms, the abundance of *P. nigra* is lower and the abundance of *S. alba* is higher. Monospecific patches of *P. nigra* marked by biogeomorphic accumulation landforms account for 25% of the total observations, compared with 10% for *S. purpurea*, and 3% for *S. alba*; while mixed patches marked by biogeomorphic accumulation landforms account for 31%. The probability test shows that biosedimentation induced by riparian vegetation is related to mixed patches and to *S. alba* monospecific patches (Table 6).

The test of independence shows that only the longitudinal gradient controls the occurrence of biogeomorphic accumulation landforms. Biogeomorphic accumulation landforms are statistically positively associated with downstream locations but not to upstream locations. The probability test shows that biosedimentation occurs farther away from the main channel (Table 7). The presence or absence of biogeomorphic accumulation landforms is significantly affected by other biotic parameters: minimal estimated age of patches, stem diameters and density (Table 7). Biogeomorphic accumulation landforms mostly occur when vegetation is older than 1 year and also displays the largest diameters and highest stem densities.

The probability of occurrence of biogeomorphic accumulation landforms is better controlled by the longitudinal gradient than by the transverse gradient (Fig. 6). A biogeomorphic accumulation landform is always developed (except for one patch) when *S. alba* is present in the patch because the species only occur downstream. In the case of *P. nigra* and *S. purpurea*, the probability of observing a biogeomorphic accumulation landform is higher on the downstream part of alluvial bars (Fig. 6a). When *P. nigra* is exclusively present in patches (monospecific stand), a greatly increasing tendency occurrence of biogeomorphic accumulation landforms from the upstream to downstream locations is observed (Fig. 6b). The Logit model yields a nonsignificant result for *S. purpurea* monospecific patches as similar numbers of patches at the upstream and central locations either with or without biogeomorphic accumulation landforms occurred. In the case of patches composed of a mixture of species, we observe a high probability of biosedimentation all along the longitudinal gradient. The Logit models representing the probability of occurrence of biogeomorphic accumulation landforms along the transverse gradient are nonsignificant for any of the three species, except for monospecific *P. nigra* patches (Fig. 6c). In this case, the probability of observing biogeomorphic accumulation landforms increases with the distance from the main channel (Fig. 6d).

The occurrence of biogeomorphic accumulation landforms is remarkably distributed on the first NMDS axis (Fig. 7). Although biogeomorphic accumulation landforms may occur at all locations, they are mainly found downstream farther away from the main channel. However, the spatial pattern of biogeomorphic accumulation landforms is not the same for the different species. We note that *S. alba* patches are always characterized by biosedimentation, but this is not the case for the two other species that can establish upstream. Young monospecific *P. nigra* patches (type 1) located at upstream or central locations do not induce the development of biogeomorphic accumulation landforms. On the contrary, *S. purpurea* monospecific patches of 2–4 years can create biogeomorphic accumulation landforms at upstream and central locations and at close or middle locations from the channel (type 2). Biogeomorphic accumulation landforms occur when monospecific *P. nigra* patches are older than 1 year or patches are composed of a mixture of species (types 3 and 4).

We also determine here the exclusive and extensive BFW for each species based on the NMDS results (Fig. 7b, c, d). The exclusive BFW allows us to isolate the effect of each species and identify the conditions that favour the capacity to affect geomorphology, while the extensive BFW includes the combined effect of species. As in the case of EA, the exclusive BFW of *P. nigra* and *S. purpurea* are entirely separated along the second axis, contrary to *S. alba* whose exclusive BFWs are superimposed onto the exclusive BFW of *P. nigra* and the extensive BFW of *S. purpurea*. The BFW of *S. alba* is fully superimposed onto its EA as it always affects geomorphology. The BFW of *S. purpurea* is slightly smaller than its EA and excludes some upstream patches. The largest difference between the exclusive BFW and EA is found for *P. nigra*. Its BFW is notably smaller compared to its EA, excluding the small upstream patches. The extensive BFWs of the three species are superimposed on the positive (right) side of the first axis.

4. Discussion

4.1. Establishment areas of the three riparian Salicaceae species

Our results show a significant variation in the location and spatial extent of the establishment areas (EA) on the alluvial bars of the Allier River for the three dominant riparian pioneer species (*P. nigra*, *S. purpurea*, and *S. alba*). *Populus nigra* is currently established at all locations of the longitudinal and transverse gradients, being the most abundant species and displaying the largest EA (Fig. 8). The only locations where *P. nigra*

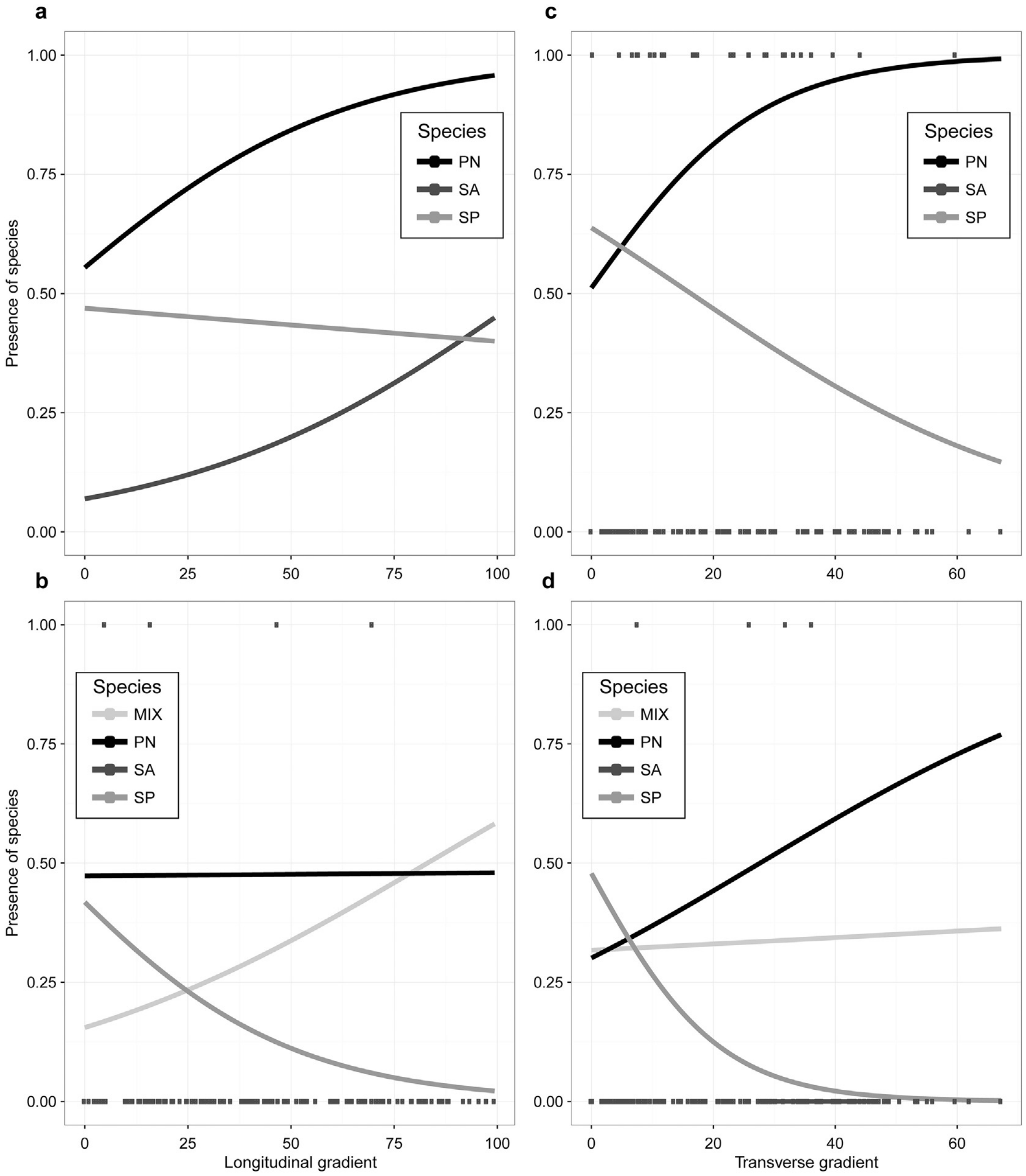

Fig. 4. Logit model representing (a) presence of the three studied species along the longitudinal gradient (upstream-downstream) and (b) monospecific and mixed patches along the longitudinal gradient (0 = upstream, 100 = downstream); (c) presence of the three species and d) monospecific and mixed patches according to the transverse gradient from the main channel to the floodplain (distance in metres).

establishment remains marginal are in the most exposed upstream areas near the main channel. This observation is in accordance with previous research that demonstrated that *P. nigra* has a high phenotypic plasticity and a strong adaptability to hydrogeomorphic disturbance (submersion, shear stress, erosion, and sediment burial) and stress (e.g., high temperature, drought) (Karrenberg et al., 2003; Chamaillard, 2011; Corenblit et al., 2014). Our observations show that *P. nigra* plants have the capacity to colonize the most exposed locations on the alluvial bars of the Allier River. However, under such conditions, the plants remain small because their aerial biomass is regularly removed or damaged during annual floods (Fig. 2). The smaller size and increased flexibility (i.e., resistance and avoidance traits sensu Puijalon et al., 2011) potentially favour the resistance of *P. nigra* individuals under highly exposed situations. This observation is in agreement with Gurnell (2014), who pointed out that hydrogeomorphic disturbances very strongly affect riparian growth within highly exposed active river tracts. Perona et al. (2012) and Garófano-Gómez et al. (2016) noted that *P. nigra* plants increase their root biomass when exposed to drag forces. Hortobágyi et al. (in press) also showed that *P. nigra* plants adapt their aboveground (e.g., a reduced size) and belowground morphological attributes (e.g., production of structural roots) to increase their resistance on the most exposed locations of the alluvial bars of the Allier River studied here.

Salix purpurea shows a smaller exclusive EA than *P. nigra*, occurring mainly in the most exposed upstream to central locations of alluvial bars, close to the main channel where monospecific patches of *P. nigra* and *S. alba* are absent (Fig. 8). *S. purpurea* is highly resistant to shear stress and uprooting and, for this reason, it is well adapted for riparian restoration (Lavaine et al., 2015), for example in gully restoration projects (Erktan and Rey, 2013). In particular, *S. purpurea* plants have biomechanical attributes (e.g., a flexible and resistant multistemmed canopy) that provide a high resistance to hydraulic constraints, prolonged submersion, and sediment burial. Close to the floodplain or

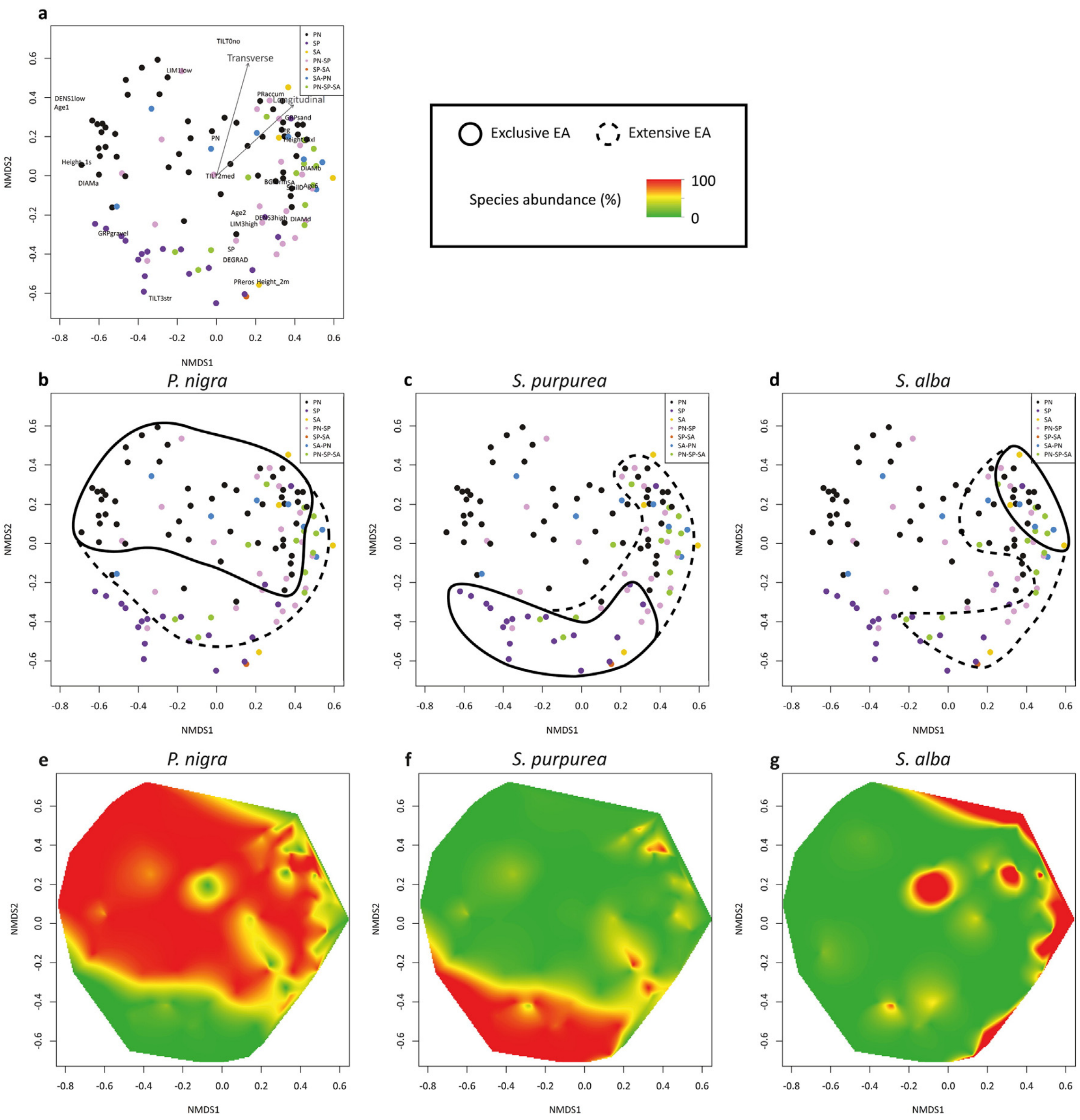

Fig. 5. (a) Results of nonmetric multidimensional scaling (NMDS) superimposed on species composition of patches and environmental fit of significant ($p < 0.01$) variables (arrows), showing distribution of exclusive and extensive EAs of (b) *P. nigra*, (c) *S. purpurea*, and (d) *S. alba* and interpolation based on species abundance: (e) *P. nigra*, (f) *S. purpurea*, (g) *S. alba*.

at downstream locations, *S. purpurea* plants mostly occur in mixed stands with the two other species but with a reduced density.

Overall, *S. alba* has a low abundance and is preferentially located on the downstream or central parts of the alluvial bars, at middle or far locations from the main channel within patches where *P. nigra* is also present, or where all three species coexist (Fig. 8). The downstream location is not only favourable for *S. alba* establishment because of a reduced exposure to hydrogeomorphic constraints but also provides better access to a higher water table connected to secondary channels located at the downstream part (alcoves sensu Curtis and Guerrero, 2015), which function as buffers against water table decline and drought during summer. In addition, fine sediments are preferentially deposited on the downstream parts of gravel bars, thus maintaining better moisture conditions than elsewhere where sediments are coarser and well drained (Pautou et al., 1985). The EA of *S. alba* on the Allier River corroborates the observations of Splunder et al. (1996) on the Rhine River in the Netherlands where *S. alba* is highly sensitive to water-table variations and drought stress occurring on gravel bars during summer. These results are also in concordance with González et al. (2012) who evaluated the mortality rate of four riparian species (*S. alba*, *P. nigra*, *P. alba*, and *Tamarix* spp.) according to variable hydrogeomorphic conditions on the Ebro River, Spain. These authors (*op. cit.*) demonstrated that *S. alba* is the most vulnerable species to drought stress related to deeper water tables, shorter flood durations and lower flood frequencies. In their experiment, González et al. (2012) also showed that *P. nigra* was vulnerable to drought stress but to a much lesser extent than *S. alba*. Using an ex situ experiment, Guilloy et al. (2011) demonstrated that *S. alba* plants respond to abrupt water table level drops with a higher mortality rate compared to *P. nigra*. Lavaine (2013) found that *S. alba* is less drought resistant than *S. purpurea*. Our results show that the specific adaptations and ecological requirements of the different species lead to a significant spatial segregation of their EAs that can be statistically mapped (Figs. 5 and 8).

The time component of patch dynamics is not explicitly included in our analysis, neither the lateral migration of the main channel nor the subsequent evolution of secondary channels and relative x, y and z positions of the patches. By including these parameters in studies such as performed on the Allier River, we could obtain supplementary

Table 5
Occurrence of biogeomorphic accumulation landforms according to the presence of each of the three species (PN = *P. nigra*, SP = *S. purpurea*, SA = *S. alba*; SD = standard deviation; letters are assigned to groups (i.e., A, B) indicating that the groups are significantly different, significant differences are indicated in bold).

Species	Parameters	Biogeomorphic accumulation landform	
		Yes	No
PN	N	70	31
	%	*55.56*	*24.6*
	Mean (%)	62.15	75.39
	SD	41.78	41.87
	Group	**A**	**B**
p-value at $\alpha = 0.05$		**0.01**	
SP	N	44	11
	%	*34.92*	*8.73*
	Mean (%)	25.01	24.49
	SD	36.28	41.94
	Group	A	A
p-value at $\alpha = 0.05$		0.15	
SA	N	25	1
	%	*19.84*	*0.79*
	Mean (%)	12.79	0.13
	SD	27.88	0.8
	Group	**A**	**B**
p-value at $\alpha = 0.05$		**0.001**	
Total number of patches	N	87	39
	%	*69.05*	*30.95*

Table 7
Occurrence of biogeomorphic accumulation landforms according to the longitudinal and transverse gradients and biotic variables (the *p*-value of X^2 and pairwise test results (> attraction, < repulsion from the variable) are indicated in grey when significant).

Parameters	Class	Biogeomorphic accumulation landform	
		Yes	No
Longitudinal gradient	Upstream	<	>
	Central	<	>
	Downstream	>	<
p-value at $\alpha = 0.05$		0.009	
Transverse gradient	Close	<	>
	Middle	>	<
	Far	>	<
p-value at $\alpha = 0.05$		0.10	
Age	1	<	>
	2	>	<
	4	>	<
	6	>	<
p-value at $\alpha = 0.05$		<0.0001	
Stem diameter	Very small	<	>
	Small	>	<
	Medium	>	<
	Big	>	<
p-value at $\alpha = 0.05$		<0.0001	
Stem density	Low	<	>
	Medium	>	<
	High	>	<
p-value at $\alpha = 0.05$		<0.0001	

information about the spatial extent of the recruitment areas of the three species. Although the Allier River is still a highly dynamic and unstable wandering/meandering river, the patches sampled in 2015 could have been recruited between 2008 and 2014 under different habitat conditions and within different locations on the alluvial bars. We need to consider that *P. nigra*, *S. purpurea*, and *S. alba* seedling recruitment generally occurs near the main and secondary channels (Mahoney and Rood, 1998). However, on the Allier River, lateral channel migration leads to a relative displacement of the established patches toward the inside, i.e., toward the floodplain, bends of the alluvial bars. A dendrochronological study would allow us to determine the exact patch ages and growth rates, leading to more precise description of the conditions of occurrence of the EAs and BFWs. In addition, a three dimensional diachronic multiscale study could provide additional information about hydrogeomorphic changes (e.g., river channel migration, secondary channel formation and adjustment, topographic changes) as well as vegetation establishment and growth, yielding a better understanding of feedbacks between riparian vegetation and hydrogeomorphic processes (Hortobágyi et al., 2017). Furthermore, we are aware that additional factors, such as microtopography heterogeneity and the deposition of large woody debris can potentially disturb the statistical model of the EA presented here (Fig. 8). For example, the accumulation of large woody debris facilitates the deposition of fine sediment, as well as the recruitment, establishment, and growth of vegetation; uprooted trees may also sprout and develop new root networks enhancing pioneer island formation (Gurnell et al., 2005). On the Allier River, the sexual regeneration strategy of *P. nigra* can sometimes be more important than its vegetative reproduction/propagation (van Oorschot et al., 2016). The sexual regeneration strategy could occasionally be favoured by deposited wood or, on well-established patches, offering a shelter against hydrodynamic forces as observed on the Frome River, UK (Moggridge and Gurnell, 2009). However, the sprouting strategy is also operative in highly exposed locations around older trees (field observations of B. Hortobágyi and P-A. Dejaifve). Beavers (*Castor fiber*) and coypu (*Myocastor coypus*) present on the Allier River may also cause vegetative propagation of the vegetation but also tree damage. Breton et al. (2014) evaluated the response of seven *Salicaceae* species (including *P. nigra*,

Table 6
Occurrence of biogeomorphic accumulation landforms according to monospecific and mixed species patches (PN = *P. nigra*, SP = *S. purpurea*, SA = *S. alba*; the *p*-values of X^2 and pairwise test results (> attraction, < repulsion from the variable) are indicated in grey when significant).

Species	Parameters	Biogeomorphic accumulation landform			
		Yes		No	
PN	N	32	<	27	>
	%	25.4		21.43	
SP	N	12	<	8	>
	%	9.52		6.35	
SA	N	4	>	0	<
	%	3.17		0	
MIX	N	39	>	4	<
	%	30.95		3.17	
p-value at $\alpha = 0.05$			0.0004		
Sum (PN+SP+SA+MIX)	N	87		39	
	%	69.05		30.95	

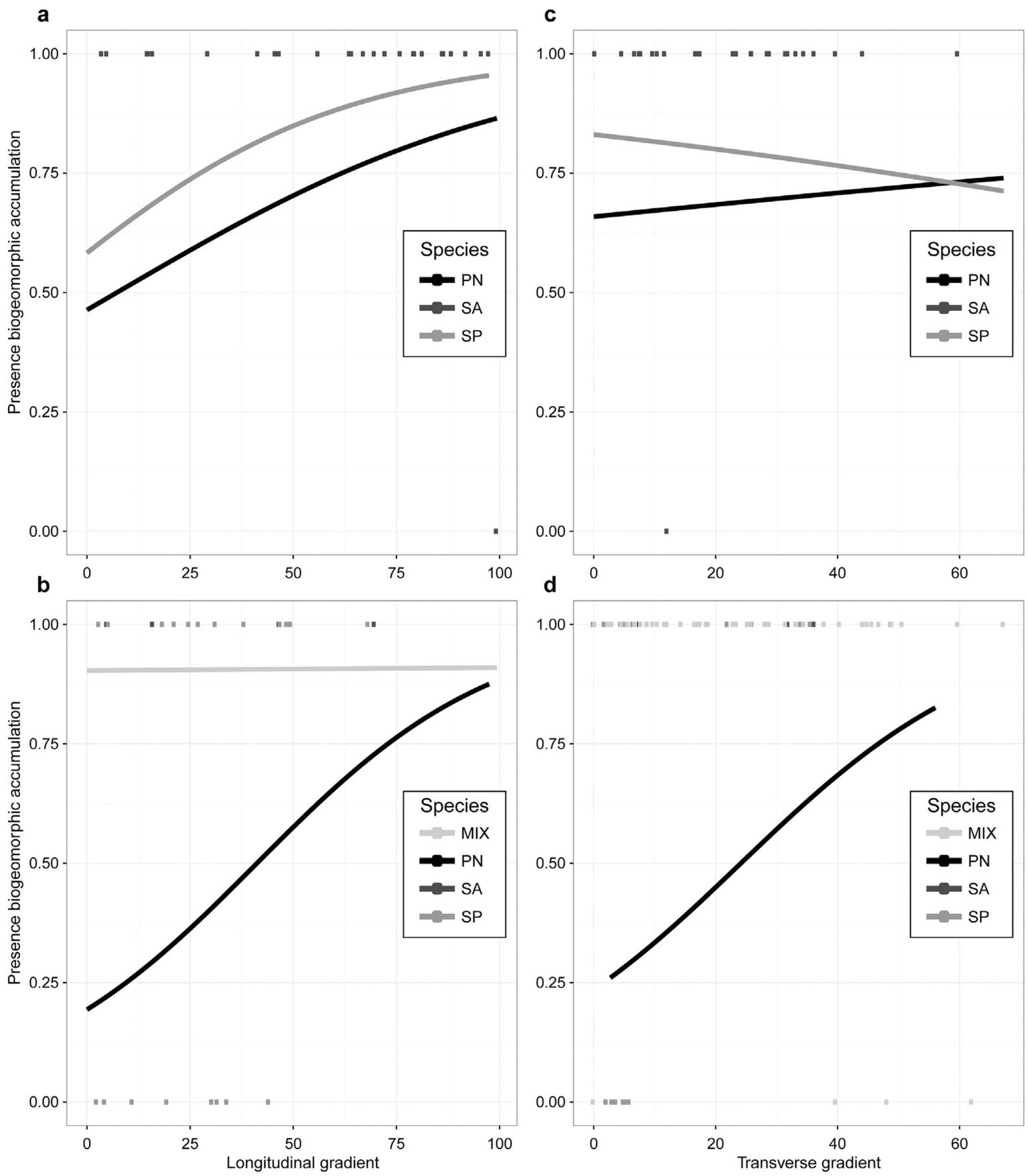

Fig. 6. Logit model representing the presence of biogeomorphic accumulation landforms with respect to (a) the simple presence of the three species and (b) monospecific and mixed patches according to the longitudinal gradient (0% upstream, 100% downstream); (c) the simple presence of the three species and (d) monospecific and mixed patches according to the transverse gradient.

S. purpurea, and *S. alba*) to high coypu browsing pressure, showing that *P. nigra* and *S. purpurea* are the least affected species. Future studies of vegetation establishment in areas where beavers and coypu occur should take these aspects into consideration.

4.2. Biogeomorphic feedback window

Our results show that resilience, i.e., the ability of fluvial biogeomorphic ecosystems such as the Allier River to retain essential processes when disturbed and maintain their structural and functional integrity before changing to another domain of attraction, is modulated by the functional response and effect traits of engineering plants that can vary between species (interspecific) and within species (intraspecific). Furthermore, the engineering effect of the species is more or less effective depending on the location along the longitudinal and transverse gradients of the alluvial bars. We suggest that interspecific diversity and intraspecific variability of functional traits related to engineer species increase biogeomorphic resilience. Indeed, the three species (or their mixture within dense patches) are developed in EAs and BFWs that are preferentially located along the longitudinal and transversal gradients. We suggest that taking account of the EA and BFW characteristics of each engineer species and their co-occurrence allows us to consider biogeomorphic resilience in terms of functional traits in contrasted geomorphological situations. In the current hydrogeomorphic context, all three species act as ecosystem engineers sensu Jones et al. (1994) because they enhance sediment trapping and landform construction. All three species thus contribute to biogeomorphic resilience on alluvial bars of the Allier River. However, biogeomorphic accumulation landforms are not present in the whole domain encompassing the EA of the three species (Fig. 8). The engineer effects of the species and their related

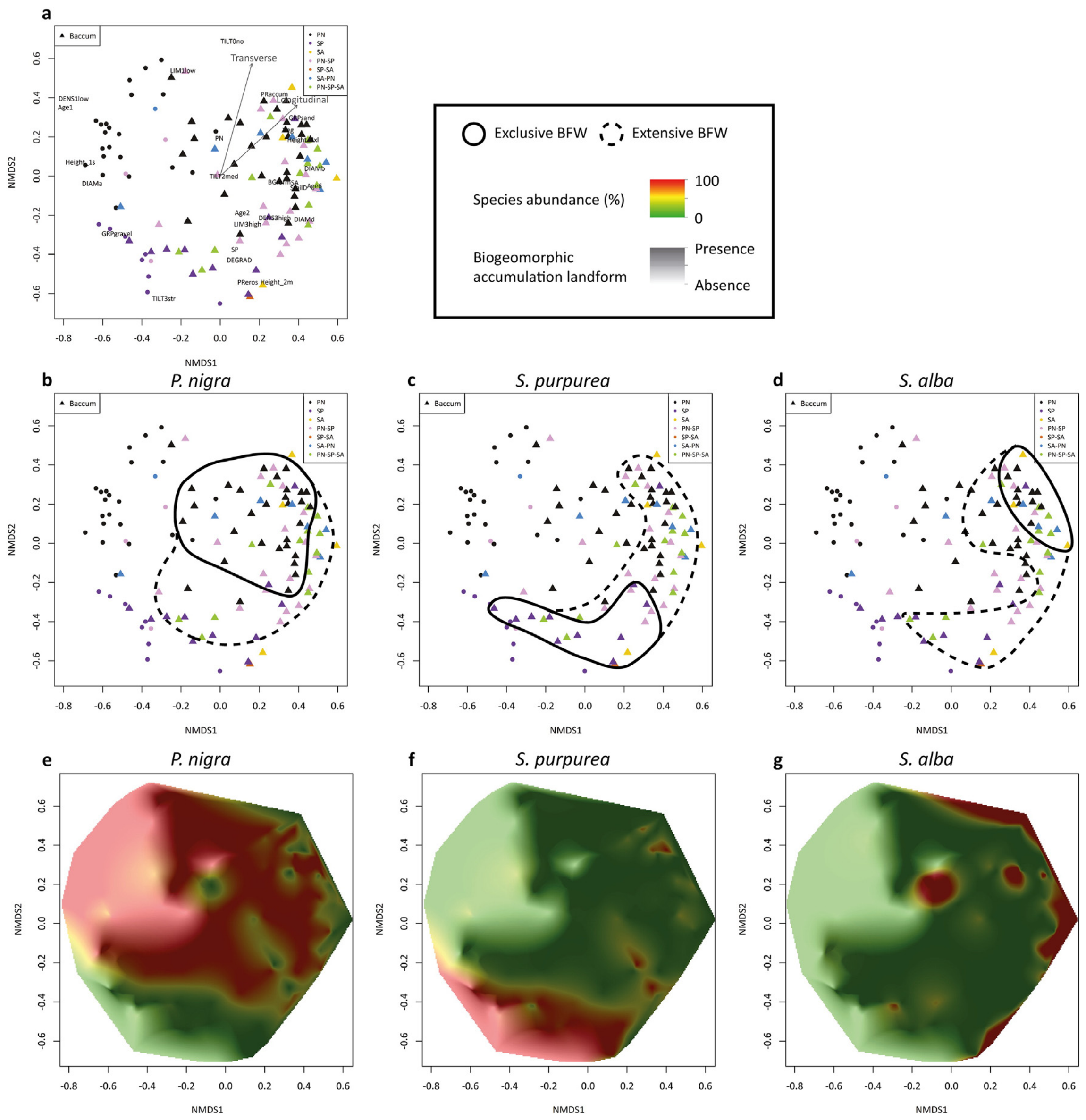

Fig. 7. (a) Results of nonmetric multidimensional scaling (NMDS) superimposed on species composition of patches, occurrence of biogeomorphic accumulation landforms, and environmental fit of significant ($p < 0.01$) variables (arrows), with distribution of the exclusive and extensive BFWs of (b) *P. nigra*, (c) *S. purpurea*, and (d) *S. alba* and interpolation based on species abundance superimposed on presence of biogeomorphic accumulation landforms. (e) *P. nigra*, (f) *S. purpurea*, (g) *S. alba*.

impact on biogeomorphic resilience varies in intensity according to the combined effects of exposure to hydrosedimentary disturbances and species physiognomy.

Populus nigra is currently the best adapted species to construct biogeomorphic landforms within the study reach of the Allier River. The BFW of this species occurs mostly in the central to downstream parts of the alluvial bars where individuals are not excessively exposed to annual floods and where they are older than 1 year. The most exposed areas of the alluvial bar, i.e., upstream locations and near the main channel, are excluded from the BFW of *P. nigra*. When present in these locations, *P. nigra* stands are generally composed of individuals with one small stem showing scarification marks related to flow damage. At less exposed locations of the central part of alluvial bars, *P. nigra* plants respond with a flexible multistemmed canopy, a higher biomass, and patch density resulting in very effective sediment trapping, i.e., a strong engineer effect. This physiognomic response of *P. nigra* in less exposed locations leads to a positive feedback between plants and landform dynamics, which results within a few years in the bioconstruction and biostabilization of wooded bars as shown by Corenblit et al. (2016a) on the channelized Garonne River, France (Fig. 2).

Within the most exposed parts of the alluvial bars on the Allier River, only *S. purpurea* plants are able to generate a BFW. Within *S. purpurea* monospecific patches, the occurrence of a biogeomorphic accumulation landform is more related to plant physiognomy (stem density, size, and diameter) rather than to the two hydrogeomorphic gradients (i.e., longitudinal and transverse). The BFW of *S. purpurea* occurs mostly all along the gradients where the canopy is well developed with a dense and multistemmed bushy shape, with stems of larger diameter. Such effects of plant morphology on sediment dynamics have been investigated in more detail in fluvial (Euler et al., 2014) and coastal systems (Bouma et al., 2013). Using a field experiment in a context of soil erosion restoration, Erktan and Rey (2013) showed that when *S. purpurea* is exposed to high sediment flow in eroded gullies, stem diameter has the strongest influence on the sediment retention capacity of the plant. When vegetation

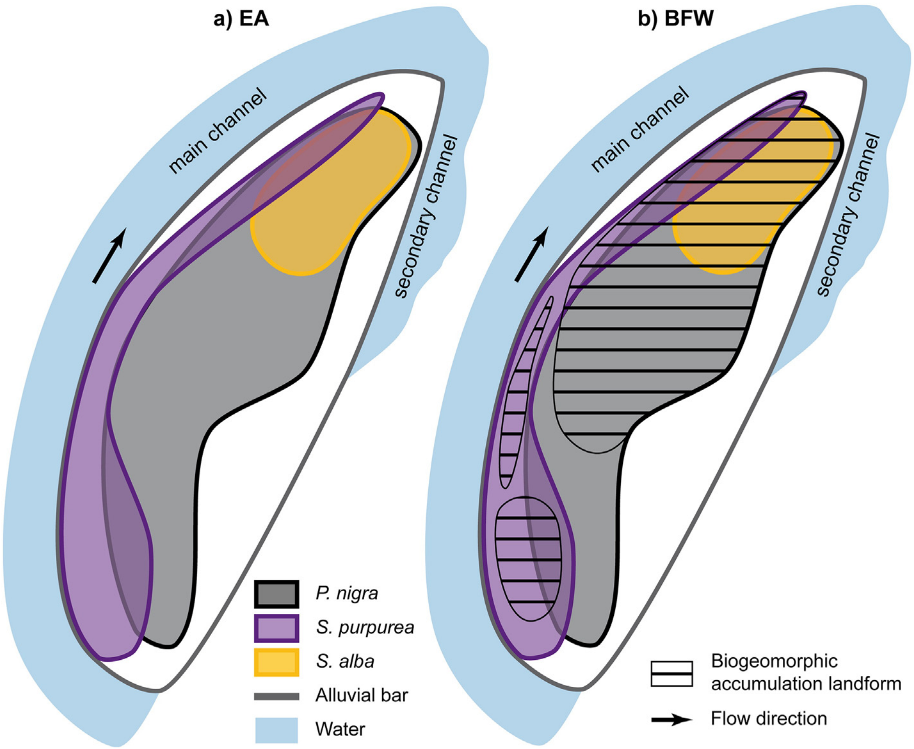

Fig. 8. Conceptual model based on statistical analysis of 16 alluvial bars of the Allier River representing (a) the establishment area and (b) the biogeomorphic feedback window of *P. nigra*, *S. purpurea*, and *S. alba*. Only the studied phases (pioneer and biogeomorphic) of the vegetation are represented in this figure.

is exposed to low sediment flow, other morphological traits, in particular related to the canopy (Burylo et al., 2012) and stem density (Erktan et al., 2012), determine the sediment trapping efficiency.

When *S. alba* is present within a patch, biosedimentation always takes place. This suggests that *S. alba* has the capacity to retain sediment but only at downstream locations near secondary channels that are intrinsically favourable for fine sediment deposition (Barsoum, 2001). Thus, our observations show that the engineer effect of *S. alba* mostly occurs at locations with an intrinsic physical predisposition for fine sediment deposition linked to flow characteristics. Hence, this species acts as a factor favouring sedimentation conjointly with natural hydrodynamic tendencies. Furthermore, *S. alba* plants always act conjointly with *P. nigra* within mixed patches as ecosystem engineer species, which makes it difficult to estimate the relative contribution of *S. alba* to biosedimentation and therefore its role in biogeomorphic landform construction and resilience.

Our observations provide some indications of how riparian engineer species can develop different response traits to hydrogeomorphic constraints, thus allowing their establishment in an unstable and fluctuating geomorphic environment, as suggested by several authors (Karrenberg et al., 2002; Lytle and Poff, 2004; Bornette et al., 2008; Naiman et al., 2008; Corenblit et al., 2015). A recent study on the same reach of the Allier River showed that young (1–2 years old) *P. nigra* plants develop different response traits depending on their exposure to mechanical stress (Hortobágyi et al., in press). *Populus nigra* developed avoidance response traits (i.e., small flexible stems and more strong structural roots) at the most exposed locations of the studied alluvial bars, which improve resistance of the plants to high energy flows. At less exposed locations, plants developed taller, less flexible stems and finer root systems. Consequently, *P. nigra* plants can only affect sediment trapping at locations where they can sufficiently increase their aerial biomass. On the other hand, *S. purpurea* plants develop response traits that result in a higher capacity to trap sediment within the most exposed locations of the alluvial bars. Kui et al. (2014) emphasized the role of plant morphological and biomechanical traits in controlling sediment trapping capacity. These authors (*op. cit.*) showed that species such as *tamarisk* trap more sediment than cottonwood because of their greater frontal area and lower maximum crown density.

In general, the occurrence or absence of a biogeomorphic accumulation landform is significantly controlled by plant physiognomic parameters such as stem diameter, height, and density (Table 7). These results also suggest that patches composed of a combination of two or all three species have a high probability of occurrence of biogeomorphic accumulation landforms because (i) these patches are mostly located on medium to less-exposed locations of the alluvial bar and (ii) they are generally dense and composed of numerous individuals older than 1 year with different morphologies and biomechanical attributes. Our observations imply that the combination of different morphological and biomechanical traits of the species within mixed patches improves the capacity of the vegetation to trap sediments, as observed within the active tract of the Tech River, France (Corenblit et al., 2009). This is also in line with previous results that suggest that the enhanced sediment trapping capacity of mixed-species patches may be linked to a greater hydraulic roughness originating from a more complex and resistant vegetative aerial structure (e.g., different stem morphologies and flexibilities, complementary crown architectures) (Kui et al., 2014). In addition, Kui et al. (2014) proposed that the sediment trapping capacity of multiple-species patches would increase in a nonlinear way in relation to growth of stem height, diameter, and crown area.

4.3. Interactions between plants

We propose that increasing functional trait diversity on alluvial bars may increase the set of possible interactions between plants. Our results show that positive interactions (facilitation) occur among the different species in the central and downstream locations of alluvial bars, resulting in an improved capacity to build landforms. In our study, we do not explicitly focus on inter- or intraspecific facilitation effects enhanced by established cohorts. The occurrence of such positive interactions between plants is likely to occur on the alluvial bars of the Allier River.

On the same study reach on the Allier River, woody pioneer riparian engineer species not only enhanced fine sediment retention but also controlled seed deposition and the potential of plant diversity resilience (Corenblit et al., 2016b). Seed deposition enhances the resilience of herbaceous mats on exposed areas of alluvial bars where they could not establish without facilitating effects. Herbaceous mats can further enhance an autocatalysed process of plant resilience by stabilizing fine substrates, as well as by trapping additional sediment and seeds. We suggest that biogeomorphic accumulation landforms induced by the three woody engineer species may favour the establishment of herbaceous plants, which also act as additional ecosystem engineers and thus contribute to the biogeomorphic succession (Corenblit et al., 2009).

4.4. Will the EA and BFW of the three species remain stable?

Changes in the frequency and magnitude of river discharge, as induced by climate change, sediment extraction, or dam construction, strongly impact riparian plant community assemblages because of their strong dependence on flow regime and sediment dynamics (Lytle and Poff, 2004). We suggest that the ecological response and related biogeomorphic resilience of the Allier River to changes in the hydrogeomorphic regime may result in shifts in the spatial distribution and extent of the EAs and BFWs of the different riparian engineer species. *Populus nigra* has the highest resilience of the three species studied here because it has a strong phenotypic plasticity. Therefore, in the current hydrogeomorphic context of a wandering/meandering style (Petit, 2006), *P. nigra* may increase in dominance as observed in the case of the channelized Garonne River (Corenblit et al., 2016a). The aboveground biomass production of *S. purpurea* is more marked when it is not exposed to severe drought stress (Lavaine et al., 2015). If the occurrence of drought periods decreases and of high flows increases, we might expect that this species could potentially extend its EA and have a greatly intensified effect on biogeomorphic landform construction. However, the hydrogeomorphic disturbance regime will most likely continue to decrease and the river will shift toward a more stable meandering system as suggested by Petit (2006). In such a context, *S. purpurea* may undergo a strong regression in the ecosystem as its EA would become fully superposed with *P. nigra*, the latter species being more competitive in terms of access to water and light. Out of three pioneer species studied here, *S. alba* is the most vulnerable to drought stress and shorter flood duration. The current geomorphic trajectory toward a meandering style, combined with an increased drought stress in summer, could make *S. alba* recruitment and establishment more difficult on alluvial bars.

5. Conclusion and perspectives

Our results lead to a clear identification of the establishment area (EA) and biogeomorphic feedback window (BFW) of three riparian pioneer species on alluvial bars of the lower Allier River. In the current hydrogeomorphic context, the three species studied here are becoming established on the alluvial bars. However, the differences in species abundance and location of the EA suggest that, under the current hydrogeomorphic conditions, *P. nigra* is favoured because it has the strongest plasticity in relation to hydrogeomorphic disturbances, water stress and scarcity. The EA of *S. purpurea* is mainly developed on the most exposed locations of the alluvial bars, while *S. alba* is found in the less exposed environments. Thus, *P. nigra* and *S. purpurea* not only have their exclusive EAs but also a common EA. Although *S. alba* does not have its own exclusive EA, this species shares its EA with *P. nigra* or with *P. nigra* and *S. purpurea*. We demonstrate that, on the Allier River, *P. nigra*, *S. purpurea*, and *S. alba* can all act as ecosystem engineers. The BFWs of these three species are strongly influenced by the upstream–downstream (longitudinal) gradient of exposure and the main channel-floodplain (transverse) gradient of connectivity. At the bar scale, the biogeomorphic accumulation landform pattern is also controlled by the functional attributes of each of the three species. *Populus nigra* and *S. purpurea* have their own exclusive EA and BFW, but the EAs and BFWs of the different species taken together are also superimposed. Thus, the total EA and BFW of all three species lead to a greater spatial extent than if only one or two of the species were present on the alluvial bars. This highlights the role of biogeomorphic functional diversity in controlling the extent and rate of fluvial landform construction.

In the light of current and future climate change, we stress the importance of considering in more detail the functional characteristics (life history traits) of pioneer riparian species, and thus, at the same time, the functional diversity of traits in riparian ecosystems. The increase of functional trait diversity is supposed to increase the probability of the occurrence of key biogeomorphic engineer species and also the possibility of positive interactions (facilitation) among species (Hooper et al., 2005). In the case of a decreased diversity of functional traits as expressed in terms of response (EA) and effect (BFW), the riparian ecosystem is expected to become less stable and resilient to natural and anthropogenic disturbances. This question of the effect of biogeomorphic functional diversity should be studied in more detail.

We also expect that changes of the hydrogeomorphic regime (e.g., caused by climate change) will be followed by adjustments of intra- and interspecific interactions. A decrease in the frequency of hydrogeomorphic disturbances may give rise to increased competition between plant species, whereas a reinforcement of hydrogeomorphic disturbances may lead, as predicted by the *stress gradient hypothesis* (Bertness and Callaway, 1994), to increased intra- and interspecific positive interactions (i.e., facilitation, or potentially intraspecific cooperation or altruism). Such interactions based on cooperation or altruism correspond to helping strategies within the same species, which could favour plant survival and growth as well as fluvial landform construction (i.e., niche construction) within riparian corridors (see part 2 this issue (Corenblit et al., accepted)).

List of acronyms

BFW	biogeomorphic feedback window
EA	establishment area
NMDS	nonmetric multidimensional scaling
PN	*Populus nigra* L.
RSS	riparian Salicaceae species
SA	*Salix alba* L.
SD	standard deviation
SP	*Salix purpurea* L.
WoO	window of opportunity

Acknowledgements

B. Hortobágyi received funding for her PhD (*Contrat de recherche*) from the French Ministry of National Education, Higher Education and Research (*Ministère de l'éducation nationale, de l'enseignement supérieur et de la recherche*). We thank Benoit Bussière for his assistance in field data collection. We thank the two anonymous reviewers and the journal editor for their valuable feedback to improve the manuscript.

References

Balke, T., Bouma, T., Horstman, E., Webb, E., Erftemeijer, P., Herman, P., 2011. Windows of opportunity: thresholds to mangrove seedling establishment on tidal flats. Mar. Ecol. Prog. Ser. 440:1–9. http://dx.doi.org/10.3354/meps09364.

Balke, T., Herman, P.M.J., Bouma, T.J., 2014. Critical transitions in disturbance-driven ecosystems: identifying Windows of Opportunity for recovery. J. Ecol. 102:700–708. http://dx.doi.org/10.1111/1365-2745.12241.

Barsoum, N., 2001. 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. http://dx.doi.org/10.1023/A:1016028730129.

Bätz, N., Verrecchia, E.P., Lane, S.N., 2015. The role of soil in vegetated gravelly river braid plains: more than just a passive response? Earth Surf. Process. Landf. 40:143–156. http://dx.doi.org/10.1002/esp.3631.

Bertness, M.D., Callaway, R., 1994. Positive interactions in communities. Trends Ecol. Evol. 9:191–193. http://dx.doi.org/10.1016/0169-5347(94)90088-4.

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 Resour. Res. 47. http://dx.doi.org/10.1029/2010WR010319.

Bornette, G., Tabacchi, E., Hupp, C., Puijalon, S., Rostan, J.C., 2008. A model of plant strategies in fluvial hydrosystems. Freshw. Biol. 53:1692–1705. http://dx.doi.org/10.1111/j.1365-2427.2008.01994.x.

Bouma, T.J., Temmerman, S., van Duren, L.A., Martini, E., Vandenbruwaene, W., Callaghan, D.P., Balke, T., Biermans, G., Klaassen, P.C., van Steeg, P., Dekker, F., van de Koppel, J., de Vries, M.B., Herman, P.M.J., 2013. Organism traits determine the strength of scale-dependent bio-geomorphic feedbacks: a flume study on three intertidal plant species. Geomorphology 180–181:57–65. http://dx.doi.org/10.1016/j.geomorph.2012.09.005.

Breton, V., Forestier, O., Guindon, O., Evette, A., 2014. Ecological restoration under pressure from invasive animal species: use of salicaceae cuttings in a river bank overrun by coypu. River Res. Appl. 30:1002–1012. http://dx.doi.org/10.1002/rra.2688.

Burylo, M., Rey, F., Bochet, E., Dutoit, T., 2012. Plant functional traits and species ability for sediment retention during concentrated flow erosion. Plant Soil 353:135–144. http://dx.doi.org/10.1007/s11104-011-1017-2.

Carpenter, S., Walker, B., Anderies, J.M., Abel, N., 2001. From metaphor to measurement: resilience of what to what? Ecosystems 4:765–781. http://dx.doi.org/10.1007/s10021-001-0045-9.

Chamaillard, S., 2011. Efficience d'utilisation de l'eau chez le peuplier noir (*Populus nigra* L.): variabilité et plasticité en réponse aux variations de l'environnement. Université d'Orléans, Orléans (PhD thesis).

Corenblit, D., Tabacchi, E., Steiger, J., Gurnell, A.M., 2007. Reciprocal interactions and adjustments between fluvial landforms and vegetation dynamics in river corridors: a review of complementary approaches. Earth-Sci. Rev. 84:56–86. http://dx.doi.org/10.1016/j.earscirev.2007.05.004.

Corenblit, D., Steiger, J., Gurnell, A.M., Tabacchi, E., Roques, L., 2009. Control of sediment dynamics by vegetation as a key function driving biogeomorphic succession within fluvial corridors. Earth Surf. Process. Landf. 34:1790–1810. http://dx.doi.org/10.1002/esp.1876.

Corenblit, D., Baas, A.C.W., Bornette, G., Darrozes, J., Delmotte, S., Francis, R.A., Gurnell, A.M., Julien, F., Naiman, R.J., Steiger, J., 2011. Feedbacks between geomorphology and biota controlling Earth surface processes and landforms: a review of foundation concepts and current understandings. Earth-Sci. Rev. 106:307–331. http://dx.doi.org/10.1016/j.earscirev.2011.03.002.

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., 2014. The biogeomorphological life cycle of poplars during the fluvial biogeomorphological succession: a special focus on *Populus nigra* L. Earth Surf. Process. Landf. 39:546–563. http://dx.doi.org/10.1002/esp.3515.

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 world-wide: biogeomorphic feedbacks along water-terrestrial interfaces. Glob. Ecol. Biogeogr. 24:1363–1376. http://dx.doi.org/10.1111/geb.12373.

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., 2016a. *Populus nigra* L. establishment and fluvial landform construction: biogeomorphic dynamics within a channelized river: biogeomorphic dynamics within a channelized river. Earth Surf. Process. Landf. 41: 1276–1292. http://dx.doi.org/10.1002/esp.3954.

Corenblit, D., Vidal, V., Cabanis, M., Steiger, J., Garófano-Gómez, V., Garreau, A., Hortobágyi, B., Otto, T., Roussel, E., Voldoire, O., 2016b. Seed retention by pioneer trees enhances plant diversity resilience on gravel bars: observations from the river Allier, France. Adv. Water Resour. 93:182–192. http://dx.doi.org/10.1016/j.advwatres.2016.02.015.

Corenblit, D., Garófano-Gómez, V., González, E., Hortobágyi, B., Julien, F., Lambs, L., Otto, T., Roussel, E., Steiger, J., Tabacchi, E., Till-Bottraud, I., 2017. Niche construction within riparian corridors. Part II: the unexplored role of intra-specific positive interactions in Salicaceae species. Geomorphology (this issue, accepted).

Curtis, J.A., Guerrero, T.M., 2015. Geomorphic Mapping to Support River Restoration on the Trinity River Downstream From Lewiston Dam, California, 1980–2011 (Open-File Report No. 2015–1047). U.S. Geological Survey, Reston, Virginia.

Dejaifve, P.-A., Esquirol, N., 2011. Quantification et répartition du bois mort échoué dans la Réserve Naturelle Nationale du Val d'Allier. Réserve Naturelle Nationale du Val d'Allier - DIREN-Auvergne, Moulins.

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. Wetl. Ecol. Manag. 7:141–153. http://dx.doi.org/10.1023/A:1008411311774.

Eichel, J., Corenblit, D., Dikau, R., 2015. Conditions for feedbacks between geomorphic and vegetation dynamics on lateral moraine slopes: a biogeomorphic feedback window. Earth Surf. Process. Landf. 41:406–419. http://dx.doi.org/10.1002/esp.3859.

Erktan, A., Rey, F., 2013. Linking sediment trapping efficiency with morphological traits of *Salix* tiller barriers on marly gully floors under ecological rehabilitation. Ecol. Eng. 51: 212–220. http://dx.doi.org/10.1016/j.ecoleng.2012.12.003.

Erktan, A., Pianu, B., Lucisine, P., Rey, F., 2012. Role of the morphology of Salix tillers barriers in marly sediment trapping efficiency in gully floor under ecological restoration: a flume experiment. EGU General Assembly Conference Abstracts, p. 1864.

Euler, T., Zemke, J., Rodrigues, S., Herget, J., 2014. Influence of inclination and permeability of solitary woody riparian plants on local hydraulic and sedimentary processes. Hydrol. Process. 28:1358–1371. http://dx.doi.org/10.1002/hyp.9655.

Evette, A., Balique, C., Lavaine, C., Rey, F., Prunier, P., 2012. Using ecological and biogeographical features to produce a typology of the plant species used in bioengineering for riverbank protection in Europe. River Res. Appl. 28:1830–1842. http://dx.doi.org/10.1002/rra.1560.

Garófano-Gómez, V., Corenblit, D., Moulin, B., Steiger, J., Abadi, M., Chaleil, P., Evette, A., Forestier, O., Garreau, A., González, E., Hortobágyi, B., Julien, F., Lambs, L., Masip, J., Ploquin, S., Voldoire, O., 2016. Black Poplar (*Populus nigra* L.) Root Response to Hydrogeomorphological Constraints: An Experimental Approach. Presented at the Eco Summit, Montpellier, France.

González, E., González-Sanchis, M., Comín, F.A., Muller, E., 2012. Hydrologic thresholds for riparian forest conservation in a regulated large Mediterranean river. River Res. Appl. 28:71–80. http://dx.doi.org/10.1002/rra.1436.

Guilloy, H., González, E., Muller, E., Hughes, F.M.R., Barsoum, N., 2011. Abrupt drops in water table level influence the development of *Populus nigra* and *Salix alba* seedlings of different ages. Wetlands 31:1249–1261. http://dx.doi.org/10.1007/s13157-011-0238-8.

Guilloy-Froget, H., Muller, E., Barsoum, N., Hughes, F.M.M., 2002. Dispersal, germination, and survival of *Populus nigra* L. (Salicaceae) in changing hydrologic conditions. Wetlands 22:478–488. http://dx.doi.org/10.1672/0277-5212(2002)022[0478:DGASOP]2.0.CO;2.

Gunderson, L.H., Allen, C.R., Holling, C.S. (Eds.), 2010. Foundations of Ecological Resilience. Island Press, New York.

Gurnell, A., 2014. Plants as river system engineers. Earth Surf. Process. Landf. 39:4–25. http://dx.doi.org/10.1002/esp.3397.

Gurnell, A., Petts, G., 2006. Trees as riparian engineers: the Tagliamento river, Italy. Earth Surf. Process. Landf. 31:1558–1574. http://dx.doi.org/10.1002/esp.1342.

Gurnell, A., Tockner, K., Edwards, P., Petts, G., 2005. Effects of deposited wood on biocomplexity of river corridors. Front. Ecol. Environ. 3:377–382. http://dx.doi.org/10.1890/1540-9295(2005)003[0377:EODWOB]2.0.CO;2.

Holling, C.S., 1973. Resilience and stability of ecological systems. Annu. Rev. Ecol. Syst. 4: 1–23. http://dx.doi.org/10.1146/annurev.es.04.110173.000245.

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. Ecol. Monogr. 75:3–35. http://dx.doi.org/10.1890/04-0922.

Hortobágyi, B., Corenblit, D., Ding, Z., Lambs, L., Steiger, J., Above- and belowground response of *Populus nigra* L. to mechanical stress within the Allier River, France. Géomorphologie: Relief, Processus, Environnement (in press).

Hortobágyi, B., Corenblit, D., Vautier, F., Steiger, J., Roussel, E., Burkart, A., Peiry, J.-L., 2017. A multi-scale approach of fluvial biogeomorphic dynamics using photogrammetry. J. Environ. Manag. 202:348–362. http://dx.doi.org/10.1016/j.jenvman.2016.08.069.

Houston Durrant, T., de Rigo, D., Caudullo, G., 2016. *Salix alba* in Europe: distribution, habitat, usage and threats. In: San-Miguel-Ayanz, J., de Rigo, D., Caudullo, G., Houston Durrant, T., Mauri, A. (Eds.), European Atlas of Forest Tree Species. Publication Office of the European Union, Luxembourg.

Isebrands, J.G., Richardson, J. (Eds.), 2014. Poplars and Willows: Trees for Society and the Environment. CABI, Boston, MA.

Johnson, C.W., 2000. Tree recruitment and survival in rivers: influence of hydrological processes. Hydrol. Process. 14:3051–3074. http://dx.doi.org/10.1002/1099-1085(200011/12)14:16/17<3051::AID-HYP134>3.0.CO;2-1.

Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. Oikos 69: 373–386. http://dx.doi.org/10.2307/3545850.

Julve, P., 2016. Baseflor. Index botanique, écologique et chorologique de la flore de France. http://perso.wanadoo.fr/philippe.julve/catminat.htm (WWW Document).

Karrenberg, S., Edwards, P.J., Kollmann, J., 2002. The life history of Salicaceae living in the active zone of floodplains. Freshw. Biol. 47:733–748. http://dx.doi.org/10.1046/j.1365-2427.2002.00894.x.

Karrenberg, S., Blaser, S., Kollmann, J., Speck, T., Edwards, P.J., 2003. Root anchorage of saplings and cuttings of woody pioneer species in a riparian environment. Funct. Ecol. 17:170–177. http://dx.doi.org/10.1046/j.1365-2435.2003.00709.x.

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 Resour. Res. 50:9366–9384. http://dx.doi.org/10.1002/2014WR015719.

Lavaine, C., 2013. Evaluation des capacités biotechniques de boutures de Salicaceae et Tamaricaceae sur un gradient de sécheresse. École normale supérieure, Lyon, France.

Lavaine, C., Evette, A., Piégay, H., 2015. European Tamaricaceae in bioengineering on dry soils. Environ. Manag. 56:221–232. http://dx.doi.org/10.1007/s00267-015-0499-8.

Lytle, D.A., Poff, N.L., 2004. Adaptation to natural flow regimes. Trends Ecol. Evol. 19: 94–100. http://dx.doi.org/10.1016/j.tree.2003.10.002.

Mahoney, J.M., Rood, S.B., 1998. Streamflow requirements for cottonwood seedling recruitment—an integrative model. Wetlands 18:634–645. http://dx.doi.org/10.1007/bf03161678.

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. 71:305–317. http://dx.doi.org/10.1007/s00027-009-9193-3.

Naiman, R.J., Latterell, J.J., Pettit, N.E., Olden, J.D., 2008. Flow variability and the biophysical vitality of river systems. Compt. Rendus Geosci. 340:629–643. http://dx.doi.org/10.1016/j.crte.2008.01.002.

Odling-Smee, F.J., Laland, K.N., Feldman, M.W., 2003. Niche Construction: The Neglected Process in Evolution. Princeton University Press, Princeton.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H., Wagner, H., 2016. vegan: Community Ecology Package.

Pasquale, N., Perona, P., Francis, R., Burlando, P., 2013. Above-ground and below-ground *Salix* dynamics in response to river processes. Hydrol. Process. 28:5189–5203. http://dx.doi.org/10.1002/hyp.9993.

Pautou, G., Décamps, H., Amoros, C., Bravard, J.P., 1985. Successions végétales dans les couloirs fluviaux: l'exemple de la plaine alluviale du Haut Rhône français. Bull. d'écologie 16 (3), 203–212 (tabl.,ill.,bibliogr).

Perona, P., Molnar, P., Crouzy, B., Perucca, E., Jiang, Z., McLelland, S., Wüthrich, D., Edmaier, K., Francis, R., Camporeale, C., Gurnell, A., 2012. Biomass selection by floods and related timescales: part 1. Experimental observations. Adv. Water Resour. 39: 85–96. http://dx.doi.org/10.1016/j.advwatres.2011.09.016.

Petit, S., 2006. Reconstitution de la dynamique du paysage alluvial de trois secteurs fonctionnels de la rivière Allier (1946-2000), Massif Central, France. Géographie Phys. Quat. 60:271–287. http://dx.doi.org/10.7202/018000ar.

Pimm, S.L., 1984. The complexity and stability of ecosystems. Nature 307:321–326. http://dx.doi.org/10.1038/307321a0.

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 Phytol. 191:1141–1149. http://dx.doi.org/10.1111/j.1469-8137.2011.03763.x.

R Core Team, 2015. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rameau, J.C., Mansion, D., Dumé, G., 2008. Flore forestière française: Plaines et collines. Institut pour le développement forestier, Paris, France.

Richter, B.D., Richter, H.E., 2000. Prescribing flood regimes to sustain riparian ecosystems along meandering rivers. Conserv. Biol. 14:1467–1478. http://dx.doi.org/10.1046/j.1523-1739.2000.98488.x.

Splunder, I.V., Voesenek, L., Vries, X.D., Blom, C., Coops, H., 1996. Morphological responses of seedlings of four species of Salicaceae to drought. Can. J. Bot. 74:1988–1995. http://dx.doi.org/10.1139/b96-238.

van Oorschot, M., Kleinhans, M., Geerling, G., Middelkoop, H., 2016. Distinct patterns of interaction between vegetation and morphodynamics. Earth Surf. Process. Landf. 41: 791–808. http://dx.doi.org/10.1002/esp.3864.