Control of sediment dynamics by vegetation as a key function driving biogeomorphic succession within fluvial corridors

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ABSTRACT: Riparian vegetation responds to hydrogeomorphic disturbances and environmental changes and also controls these changes. Here, we propose that the control of sediment erosion and deposition by riparian vegetation is a key geomorphological and ecological (i.e. biogeomorphic) function within fluvial corridors. In a 3 year study, we investigated the correlations between riparian vegetation and hydrogeomorphic dynamics along a transverse gradient from the main channel to the floodplain of the River Tech, France. Sediment erosion and deposition rates varied significantly along the transverse gradient as a function of the vegetation biovolume intercepting water flow. These effects, combined with the extremely strong mechanical resistance of pioneer woody structures and strong resilience of pioneer labile herbaceous communities, *Populus nigra* and *Salix* spp., explain the propensity of biogeomorphic succession (i.e. the synergy between vegetation succession and landform construction) to progress between destructive floods. This geomorphological function newly identified as an 'ecosystem function' *per se* encompasses the coupling of habitat and landform creation, maintenance and change with fundamental ecosystem structural changes in space and in time. Three different biogeomorphic functions, all related to the concept of ecosystem engineering, were identified: (i) the function of pioneer herbaceous communities to retain fine sediment and diaspores in the exposed zones of the active tract near the water resource, facilitating recruitment of further herbaceous and *Salicacea* species; (ii) the function of woody vegetation to drive the construction of forested islands and floodplains; and (iii) the function of stabilised riparian forests to act as 'diversity reservoirs' which can support regeneration after destructive floods. Overall, this study based on empirical data points to the fundamental importance of sediment flow control by pioneer riparian vegetation in defining fluvial ecosystem and landform organisation in time and in space. Copyright © 2009 John Wiley & Sons, Ltd.

KEYWORDS: biogeomorphic function; ecological function; riparian vegetation; ecosystem engineers; seed bank; fluvial landforms; biogeomorphic succession; sediment dynamics

Introduction

'Function' has become a fundamental concept in ecology. It can be considered to be what an organism, a species, a community or an ecosystem does in the context of its surrounding environment. Current biogeochemical functions such as nutrient and water cycling, organic matter production and decomposition, and community respiration have been identified as the major 'ecological functions' driving ecosystem and biodiversity dynamics (Naeem and Wright, 2003). Some authors have also invoked biodiversity *per se* as an ecological function (Baskin, 1994; Hooper and Vitousek, 1998), due to its implications for flux regulation, system stabilisation and performance. However, there are many different meanings and uses of 'function' in ecology (Bradshaw, 1987; Calow, 1987; Keddy,

1992; Schultze and Mooney, 1994; Loreau *et al.*, 2001, 2004; Jax, 2005). Whereas most ecological functions directly involve biological metabolism, other mechanisms of material, energy or information (i.e. genes, diaspores, individuals) transfer and storage between ecosystem compartments indirectly involve biological activity. Such indirect controls on ecological fluxes through habitat creation, construction or modulation by living organisms, embrace more than just direct trophic functions and are termed 'ecosystem engineering' by ecologists (Jones *et al.*, 1994, 1997; Cuddington *et al.*, 2007) and 'niche construction' by evolutionary biologists (Odling-Smee *et al.*, 2003).

Sediment is a key component of habitats and of landform dynamics, i.e., the object of study for geomorphologists. Biogeomorphic approaches are recently investigating feed-

back mechanisms between biota, topography and landscape dynamics (Corenblit *et al.*, 2008; Murray *et al.*, 2008; Francis *et al.*, in press). Abiotic-biotic feedbacks occur when organisms' morphology and life-history (e.g. reproduction, dispersion, and growth) are regulated by physical processes, and when in turn these physical processes are to some extent regulated by the organisms' activity. This interdisciplinary approach integrates concepts such as the concept of 'ecosystem engineering' (Jones *et al.*, 1994) from ecological sciences and the concept of self-organisation from physical sciences (Bak *et al.*, 1988). New concepts such as 'functional ecomorphology' (Fisher *et al.*, 2007) and 'biogeomorphic succession' (Corenblit *et al.*, 2007) contribute to the consideration of functional processes in a biogeomorphic perspective by linking form and function and by focusing on reciprocal causation between them. Such concepts represent an opportunity to investigate how geomorphology provides a structural template that shapes, and is shaped by ecological processes.

As pointed out by Fisher *et al.* (2007), running water ecosystems illustrate several principles governing the interaction of landscape form and ecological function. Whereas the control of sediment dynamics by wetland plants has been identified as an important component of intertidal ecosystem function (Lee and Partridge, 1983; Pasternack and Brush, 1998; Bos *et al.*, 2007; van Hulzen *et al.*, 2007), the effect of riparian vegetation on sediment erosion and deposition within fluvial systems has been studied mainly from the geomorphic perspective of landform dynamics (Nanson and Beach, 1977; Gurnell *et al.*, 2001; Steiger *et al.*, 2001a; Cotton *et al.*, 2006; Heppell *et al.*, 2009) Riparian habitat structure, water flow variability and sediment deposition and erosion were generally considered as limiting factors and as disturbance in the ecological literature (Franz and Bazzaz, 1977; Naiman and Décamps, 1997; Edwards *et al.*, 1999; Lenssen *et al.*, 2000; Amoros and Bornette, 2002). Some geomorphologists have started recently to focus their attention on feedback between form and function in fluvial ecosystems considering that geomorphology controls riparian vegetation dynamics, and riparian vegetation controls geomorphology (Bendix and Hupp, 2000; Hupp and Bornette, 2003; Gurnell *et al.*, 2000, 2005; Parsons and Thoms, 2007; Francis *et al.*, in press). In particular, they have considered explicitly feedback loops between water flow, sediment dynamics, fluvial landforms and riparian vegetation as part of riparian ecosystem function and change in time and space. Fluvial biogeomorphic studies suggested that the geomorphic effects (flow resistance, sediment stabilisation and accretion) and biomechanical and life history responses (mechanical resistance, reproduction, dispersion, and growth) of riparian vegetation within and between floods may represent key controls on riparian ecosystem and landscape dynamics. Thus, the effects of riparian vegetation on sediment erosion/deposition dynamics may form a biogeomorphic function regulating conjointly succession, biodiversity and landform dynamics within fluvial corridors (Corenblit *et al.*, 2009).

While it is well known that vegetation stabilises substrate and encourages sediment retention, unanswered questions relative to the identification of riparian vegetation control on sediment erosion/deposition dynamics as a key biogeomorphic function include:

(i) Do herbs, shrubs and trees influence hydrogeomorphic processes differently to one another; specifically do they influence sediment deposition and accretion differently?

(ii) Which has the greater influence on the magnitude of sediment deposition and erosion: biological structures (plant morphotypes) or location of stands along the hydrogeomorphic transverse gradient from the main channel to the floodplain?

(iii) What are the resistance and resilience of vegetation according to a quasi-annual (2 to 3 year return period) flood regime?

(iv) Can the interactions between sediment and vegetation be described as a positive feedback driving ecosystem functioning and landform dynamics where plants encourage fine sediment deposition which facilitates plant recruitment and establishment?

To answer these questions, a study based on correlation analyses was conducted on the River Tech, southern France, which assessed underlying feedbacks between vegetation communities and hydrogeomorphic dynamics along a gradient from main channel to floodplain; and the extent to which control of fluvial sediment dynamics by riparian plants may be considered a key biogeomorphic function in relation to habitat and landform adjustments and associated plant succession.

Material and Methods

Study area

The gravel bed River Tech, Western Pyrenees, France, is 85 km long and drains a Mediterranean-mountainous catchment area of 750 km². The river has a pluvio-nival flow regime with a mean annual discharge of 9·1 m³ s⁻¹ near the river mouth, high flows from April to May and November to January (10–13 m³ s⁻¹) and low flows between July and September (4–5 m³ s⁻¹). Large flash floods frequently occur in autumn when riparian vegetation is fully developed. The largest recorded flood, in October 1940, reached a peak discharge of 2500 m³ s⁻¹ in the piedmont zone according to the discharge data of the Departmental Direction of Agriculture and Forest – DDAF – (gauging station 3 km upstream of study site number one).

The River Tech is dynamic in comparison with many European rivers, maintaining a diverse landscape mosaic in several sections of its piedmont zone, from which two study sites (site 1: 42°29′ N, 2°45′ E; site 2: 42°31′ N, 2°50′ E, Figure 1) 12 km apart, were selected. These 800 m long sites were chosen because they enclosed a 100 m wide active tract and a 100 m wide riparian margin, incorporating convex alluvial bars and ten broad vegetation types (Table I) organised along a transverse successional/disturbance gradient from the main channel to the floodplain. These two sites are representative of the piedmont zone of dynamic Mediterranean fluvial systems. Within each site, observations were undertaken along a representative transect (Figure 1).

During the 3 year study (2002 to 2004), five floods occurred, each with a 2 to 3 year return period (Figure 2). Floods of this and larger return periods are recognised as important influences on active tract morphological changes (Osterkamp and Hedman, 1982). Therefore, these floods formed a suitable context in which to investigate feedbacks between vegetation communities and erosion/deposition dynamics.

Definition of distinct vegetation types and groups

We investigated changing impacts (control of erosion/deposition) and responses (resistance and resilience) of vegetation communities in relation to physiognomy and floristic compo-
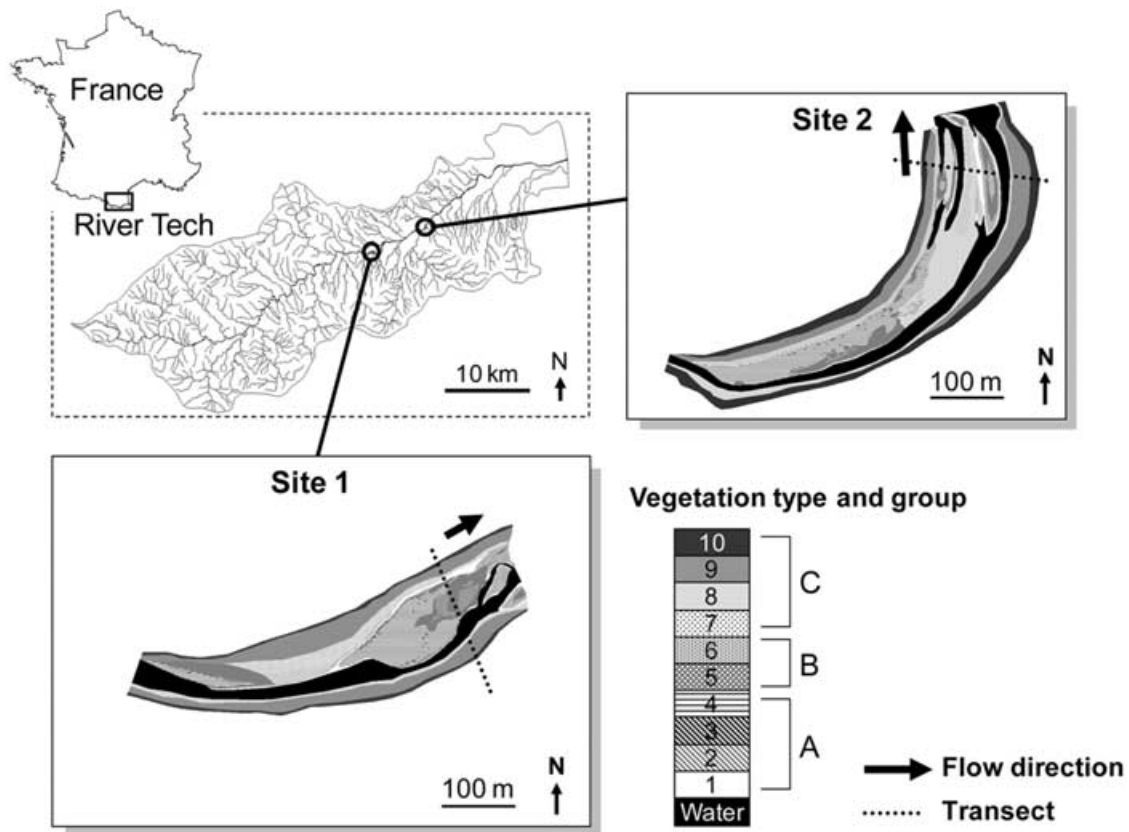
Figure 1. Location map and study sites. For description of vegetation types and groups see text and Table I, II and III.
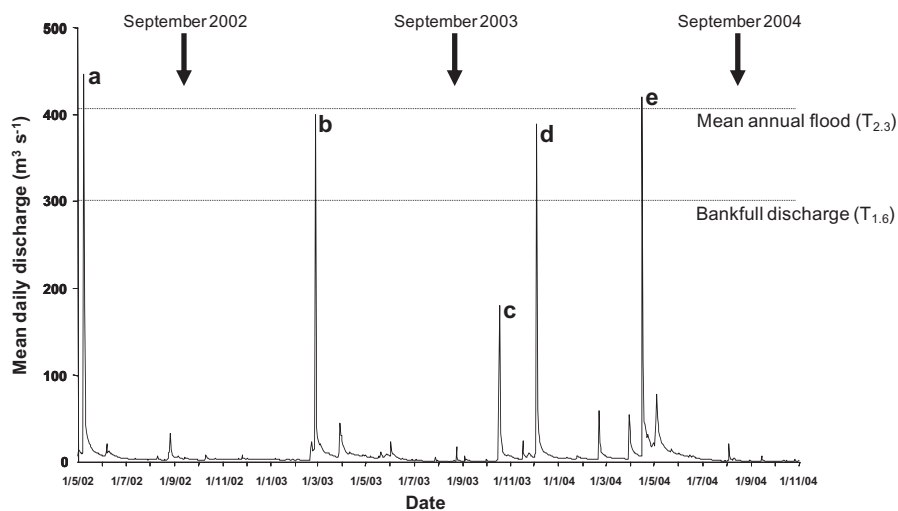

Figure 2. Daily discharges (m³ s⁻¹), flood events (a to e) and the sampling periods between May 2002 and January 2004 on the River Tech. $T_{1.6}$ corresponds to the theoretical bankfull discharge (return period of 1·6 years) and $T_{2.33}$ to the mean annual flood (return period of 2·33 years).

sition. A first task was to distinguish different vegetation types and groups (Wilson, 1999; Naeem and Wright, 2003) at the start of the study as a framework for the research. Vegetation communities were classified at the same time in September 2002, when they were fully developed. Ten types within three groups, (A) herbs and forbs, (B) shrubs and young trees, (C) adult trees, were defined according to general physiognomy (Table II) and floristic composition (Table III). Floristic composition of each type was recorded within 10, randomly positioned, 2 × 2 m plots (total, 200 plots), using the European

Flora (Tutin *et al.*, 1980) and local Kerguelen's flora (Kerguelen, 1998). Diversity indices (species richness: *s*, Mean Shannon Diversity index: *H'*) were calculated. Relative elevation (m above mean low water stage), surface and subsurface sediment grain size (mm), duration (number of days) and frequency (occurrence) of submersions per year were estimated for every plot to summarise hydrogeomorphic characteristics over the study period in relation to the initial vegetation types (Table IV). Submersion duration and frequency were deduced from the relation between water height based on repeated

Table I. Ecological and hydrogeomorphic description of the ten vegetation types observed on the two study sites

Type	Status	Spatial location	Environmental constraints (disturbance/stress)
1	Pioneer hygrophilous and dense herbaceous community (cf. Table III for floristic composition)	Within the active tract, on the immediate margins of wet channels (main and secondary channels)	Highly disturbed (cf. Table IV for detailed hydrogeomorphic parameters) Submerged during a large part of the year
2	Pioneer hygrophilous and dense herbaceous community differing from type 1 mainly through a larger range of scarce species including some that tolerate hydric stress	Within the active tract, on the margins of wet channels (main and secondary channels)	Highly disturbed Regularly and durably submerged
3	Pioneer herbaceous transition community including a large range of scarce species adapted to high soil moisture contents and flooding and also tolerating hydric stress	Within the active tract, on the transition between margins of wet channels (main and secondary channels) and alluvial gravel bars	Highly disturbed Regularly submerged
4	Pioneer meso-hygrophilous and xeric sparse herbaceous community	Within the active tract, on the less frequently submerged and well drained areas of alluvial gravel bars without ligneous vegetation	Disturbed once a year by annual floods Dryness in summer caused by low flows and drought Huge temperature amplitudes
5	Transition stage between pioneer herbaceous and pioneer shrubby (mainly young *Populus nigra* L.)	Within the active tract, on drained alluvial bars with a frequent wet and dry alternation	Disturbed once a year by annual floods
6	Pioneer shrubby stage (mainly young *Salix alba* L., *Salix eleagnos* L. and *Populus nigra* L.)	Within the active tract, on alluvial bars with a frequent wet and dry alternation	Disturbed once a year by annual floods
7	Swampy pioneer/post-pioneer forest stage (mainly adult *Alnus glutinosa* Gaert.)	Within the active tract and immediate margins, on the banks, islands and floodplains with high soil moisture and stagnant waters	Disturbed once a year by annual floods
8	Pioneer/post-pioneer riparian forest (mainly adult *Salix alba* L. and *Populus nigra* L.)	Within well drained zones of islands or immediate margins	Disturbed once a year by annual floods
9	Post-pioneer riparian forest (mainly adult *Populus nigra* L.)	On the high drained levels of the floodplain	Rarely disturbed
10	Post-pioneer riparian forest (mainly adult and senescent *Populus nigra* L. mixed with *Arundo donax* L.)	On the highest well drained level of the floodplain, at the transition with the terrestrial zone	Rarely/never disturbed

measurements between 2002 and 2004 on the transects, and the daily discharges recorded at the gauging station 3 km upstream of site 1. Daily discharges recorded between 1964 and 2004 were then used to calculate duration and frequency statistics over a 40 year period for each vegetation type.

Sampling design for change analysis

Field investigations were conducted at the same time in September 2002, 2003 and 2004, coinciding with maximum biomass development and low flows, to establish vegetation effects on net sediment erosion/deposition dynamics and responses of the vegetation types as a result of flood submergence and sediment erosion/deposition. Observations were made along one transect (~150 m) within the active tract and perpendicular to the main channel at each study site (Figure 1). Each transect was surveyed topographically using a ZEISS REC ELTA 14™ total station (Carl Zeiss AG) to a precision of ≤0·5 cm. Ecological and geomorphic parameters were measured within plots (57 at site 1; 54 at site 2) spaced at 6 m intervals along the transects using a 2 × 2 m removable, graduated, rigid aluminium frame (Figure 3a), subdivided into a regular 0·2 m mesh defining 100 sampling points (Figure 3b). Iron stakes (1 m length) driven into the substrate guided precise

relocation of the plots. The immediate surroundings of each plot were also documented using high resolution digital photographs. These photographs coupled with field mapping were taken up to 15 m upstream of the transects in the flow axis from each sample plot and gave information on presence or absence of obstacles to flow within 15 m upstream of the plot and estimates of vegetation cover, density, height and biovolume in the 2 × 2 m area immediately upstream of the plot.

Parameters quantifying ecological and hydrogeomorphic correlations

Ground-projected area of low strata (herbs, shrubs and young trees <1 m), intermediate strata (shrubs and trees between 1 to 5 m), and high strata (trees >5 m); absolute and relative coverage of plant species; species richness; mean Shannon diversity index; and individual density (number of stems) of adult plants and seedlings were recorded for each 2 × 2 m plot during September 2002, 2003 and 2004.

Four indices quantified the potential impact of vegetation on sediment dynamics (plant cover (m²), mean stem height (cm), mean stem diameter (mm), and intercepted biovolume (m³)). Mean stem height (m), and diameter (mm – measured by precision calliper) of each species were estimated from

Table II. Multivariate seriation on the dominant species (relative percentage vegetation cover >0·1). Bold numbers indicate values >1%). The ordination reflects schematically a transverse gradient from pioneer herbaceous hygrophilous communities (on the left) to drained post-pioneer riparian forest communities (on the right).

Dominant species	Type									
	1	2	3	4	5	6	7	8	9	10
Arundo donax L.	0·74				0·18	0·97	**4·49**	**7·46**	**2·78**	**25·77**
Brachypodium sylvaticum (Huds.) P. Beauv.	0·73		0·20	0·15	0·98	0·18	0·77	0·43	**2·43**	0·72
Populus nigra L.	**2·78**	0·29	0·14	0·14	**4·88**	**16·89**	**9·92**	**23·29**	**32·97**	**29·59**
Urtica dioica L.					0·17	0·80	**1·11**	0·35	0·35	0·72
Robinia pseudoacacia L.		0·48	**1·88**	0·24	0·97	**2·53**	**3·73**	**4·25**	**1·73**	**7·83**
Veronica hederifolia L.							**2·22**	**1·11**	0·98	0·20
Impatiens balfourii Hook. f.		0·30	0·17		0·15	0·23	**9·71**	**1·29**	0·42	
Rubus ulmifolius Schott					**3·86**	0·22	**1·38**	0·35	**3·18**	**2·26**
Salix purpurea L.	0·56	0·15			0·15	**1·92**	0·64	0·16	**4·76**	
Rubus caesius L.				0·70	**14·68**	0·45	**3·67**	**1·13**	**11·67**	**1·79**
Salix alba L.	**2·42**	**2·24**	**1·79**	**4·89**	**2·86**	**28·03**	**3·81**	**41·66**	**1·95**	0·63
Salix fragilis L.	0·26	0·15	0·81			**1·59**	**1·54**		0·57	0·51
Alnus glutinosa (L.) Gaert.	**4·91**	**2·15**	0·53	0·12	**1·83**	**1·64**	**46·72**	0·21	0·77	
Piptatpherum miliaceum (L.) Coss.		0·40	0·18	0·17	**5·93**	0·17		0·93	0·48	0·63
Helianthus rigidus (Cass.) Desf.	0·59	0·34	0·42	0·41	**5·84**	**4·33**	0·15		0·76	0·15
Artemisia vulgaris L.			0·94	0·57	0·33	**1·58**	0·20		0·38	0·16
Pastinaca sativa Mill.			0·14	0·90	**1·42**	0·80			0·17	0·21
Senecio inaequidens DC.		0·53	**1·35**	**1·00**	**11·82**	0·93				0·21
Artemisia verlotiorum Lam.		0·19	0·56	**7·99**	0·15	**3·97**		0·16		0·38
Saponaria officinalis L.		0·34	**1·43**	**1·83**	**6·63**	**1·37**				0·41
Buddleja davidii Franchet		0·11	0·74	0·76	**1·56**	0·67	0·31		0·17	0·13
Artemisia campestris L.		0·90	0·12	**2·73**	0·97	0·51		0·11		0·28
Salix eleagnos Scop.	**1·58**	**2·58**	0·39	0·33	0·25	**7·57**	0·37			
Sorghum halepense (L.) Pers.	0·60	0·16	0·26	0·32	**1·24**	0·78	0·20	0·71		0·18
Chenopodium album L.		0·70	**1·19**	**2·87**	0·92	0·62				0·11
Xanthium strumarium D. Löve	0·60	**1·52**	**1·25**	0·95	**3·93**	0·86		0·40		
Melilotus albus Medik.	0·98	0·62	0·58	0·64	**1·19**	0·25		0·40		0·20
Conyza floribunda Kun.	0·60	0·39	0·82	0·39	0·84	0·13				0·31
Conyza bonariensis (L.) Cronq.	0·60	0·27	0·99	0·24	0·97	0·18	0·20			0·45
Polygonum persicaria Hill	0·18	0·51	0·88	**1·35**	0·37	0·86				0·3
Verbena officinalis L.	0·79	0·14	0·15	0·87	0·19	0·80				0·56
Chenopodium ambrosioides L.	0·12	**1·12**	**1·82**	**1·79**	0·21	0·26				
Cyperus eragrostis Lam.	**21·25**	**17·84**	**12·94**	0·17	**3·26**	0·77	0·39			0·2
Polygonum lapathifolium (L.) Gray	**1·94**	**7·31**	**7·32**	0·44	0·36	0·21	0·35			
Lythrum salicaria L.	**1·33**	**1·16**	0·27		0·17	0·80	0·24			
Bidens frondosa L.	**8·42**	**4·28**	**5·68**	0·69	0·24	0·38	0·48			
Lycopus europaeus L.	**1·39**	**1·13**	**1·65**		0·18	0·80	0·99			
Echinocloa crus-galli (L.) P. Beauv.	**6·89**	**9·75**	**4·95**	0·28	0·27	0·15	0·40	0·40		0·5
Polygonum hydropiper (L.) Spach	0·92	**1·66**	0·88				0·20			
Paspalum paspalodes (Mich.) Scrib.	**5·98**	**4·94**	**1·52**				0·20			
Typha latifolia L.	**4·32**	**1·98**	0·11							

individual plants in five sub-samples of 0·2 × 0·2 m per homogeneous plant patch and for all isolated individuals within the 2 × 2 m plots. The overall biovolume (m³) intercepted by the flow was estimated as vegetation coverage (m²) × water height (m) when the vegetation was only partly submerged, and as vegetation coverage (m²) × mean plant height (m) when the vegetation was fully submerged. The intercepted biovolume was also estimated for 2 × 2 m areas immediately upstream of the main sample plots to encompass the upstream biogeomorphic context. In all statistical analyses, the intercepted biovolume was represented by the sum of the above biovolumes (on the transect plot and in the upstream area – a ground area of 8 m²). Long distance (up to 15 m upstream) drag effects of vegetation (single trees, woody debris) and other obstacles (e.g. boulders) were identified as a qualitative factor in statistical analyses (indicated by 'dr' after the vegetation unit code, e.g. in Figures 6 and 8).

Net sediment erosion/accretion rates (m year⁻¹), between September 2002–2003 and September 2003–2004 were also measured in the 2 × 2 m plots located along the transects. One corner of the sampling frame was positioned on the geo-referenced benchmark (iron stake) and the frame was then levelled using four spirit levels, one on each side of the frame (Figure 3c). A 1 m graduated metal stem, sliding vertically and horizontally on a graduated bar mounted on the graduated frame, measured the difference in elevation (m) between the bar and the substrate surface across a regular grid of 100 points. Elevation of the substrate was calculated with reference to the benchmark, Digital elevation models (DEMs) were developed from the 100 measured points, and differences between DEMs quantified net erosion/accretion between measurement dates.

Surface sediment texture was also determined each September at the 100 sample points within each plot using

Table III. Classification of vegetation types into three major groups and associated morphological traits based on observations from a field campaign in summer 2002. Low strata: <1 m; intermediate strata: 1–5 m; high strata: >5 m. The morphological traits are based on observations from ten sample (2 × 2 m) plots for each vegetation type. Standard deviation is indicated for each variable.

Vegetation type	Vegetation group	Morphological traits								
		Low strata cover (%) within quadrat	Intermediate strata cover (%) within quadrat	High strata cover (%) within quadrat	Low strata mean stem height (cm)	Intermediate strata mean stem height (cm)	High strata mean stem height (cm)	Low strata mean steam diameter (mm)	Intermediate strata mean steam diameter (mm)	High strata mean steam diameter (mm)
1	A: herbs and forbs	85 ± 2.4	0	0	28 ± 67.5	0	0	4.2 ± 0.4	0	0
2		78 ± 3.5	2.1 ± 1.3	0	34 ± 12.8	101 ± 38.2	0	3.8 ± 0.2	12 ± 2.2	0
3		65 ± 9.6	7.2 ± 2.1	0	45 ± 13.4	98 ± 24.0	0	4.2 ± 0.3	11 ± 2.8	0
4		3 ± 10.2	0	0	36 ± 15.3	0	0	3.3 ± 0.3	0	0
5	B: shrubs and young trees	68 ± 3.8	45 ± 13	0	35 ± 13.0	325 ± 40.5	0	4.2 ± 0.6	28 ± 6.0	0
6		15 ± 1.4	89 ± 5.2	0	45 ± 18.5	445 ± 135.6	0	2.6 ± 0.5	38 ± 18.6	0
7	C: adult trees	14 ± 12.4	0	95 ± 5.6	52 ± 8.5	0	817 ± 222	4.3 ± 1.4	0	112 ± 63.2
8		25 ± 4.7	0	86 ± 6.5	45 ± 6.5	0	890 ± 325	4.2 ± 0.7	0	115 ± 72.0
9		45 ± 12.7	0	100	85 ± 6.5	0	1290 ± 319	4.5 ± 2.7	0	220 ± 90.5
10		32 ± 13.7	35 ± 12.8	100	68 ± 18.5	462 ± 112.0	1600 ± 400	4.6 ± 1.1	32 ± 0.2	340 ± 126.3

standard methods (Wolman, 1954; Rice and Church, 1996). Large and small particle axes (mm) above 2 mm were determined with a precision calliper. In order to determine the thickness of the fine (i.e. <2 mm) sediment layer, the characteristics (i.e. the difference between sand or coarser sediment) of subsurface sediment texture was determined each September in a patch immediately downstream of each plot based on 4 bulk samples taken using a coarse sediment auger to a depth of 0.5 m.

Direct measurements of flow properties and sediment loads across the study transects were impossible because of high flow velocities and turbulences during the flood events on the River Tech. Instead, maximum flow depth (m) was used as the main hydrological indicator and was recorded within the active tract using three complementary methods: (i) fine organic and mineral particles trapped on rough carpet strips (0.05 m wide, 3 m high) fixed on tree trunks along the transects clearly delineated a high water mark; (ii) perforated plastic tubes (0.03 m diameter, 2.5 m high) containing carbon powder acted as crest stage gauges, marking the maximum depth of flood flows on extractable wood stems (Miller and Leopold, 1961); and (iii) any natural high water marks left by floods were recorded by topographic survey (Wolman, 1971).

To examine associations between seed bank structure (seed abundance, species richness), extant vegetation and geomorphic dynamics (sediment erosion/deposition rates), subsurface cores of 10 cm³ were sampled in September 2002 along both study transects. Four replicates were collected just outside each plot (total, 148 samples) to avoid plot disturbance. Samples were dried at 70°C for 48 h, sieved using a 200 μm mesh, and the retained fraction was elutriated to collect only the organic components. Seeds were sorted and identified by hand using a stereomicroscope and the ECOLAB Laboratory seed reference collection.

Data analysis

A cluster analysis was performed on the floristic data (relative abundance) collected in September 2002, representing the reference state for this study. The cluster analysis was performed using the Bray–Curtis similarity index, recommended in the case of abundance data (Gower and Legendre, 1986). Non-parametric ANOSIM (analysis of similarities) used Bray–Curtis distance to test for significant differences between floristic groups (Clarke, 1993). A multivariate seriation (Brower and Kyle, 1988) reorganised the floristic data matrix to concentrate species presence along the table diagonal. Spatially proximate vegetation types that demonstrated a high degree of similarity were grouped into single types prior to statistical analysis of change.

Hydrogeomorphic and ecological variables were measured and compared according to the vegetation types. The statistical significance of any differences between groups was tested using one-way and two-way analyses of variance (ANOVA). When comparing data from different dates, ANOVAs were performed with repetitions. Comparisons of the seed bank structure (species richness and seed abundance) between types were performed with ANOVAs on log-transformed data. The Tukey HSD test (Zar, 1996) was used for *post hoc* multiple comparisons between observed means. All variables were examined for normality and heterogeneity of variance and all statistical tests were considered significant with alpha = 0.05. Vegetation types that were not exposed to any hydrogeomorphic disturbances during the study were excluded from statistical analyses of change.

Table IV. Hydrogeomorphic characteristics associated with the vegetation types. Frequency and duration of submersion were calculated for 10 plots within each vegetation type between January 2002 and December 2004. Vertical subsurface profiles show sediment structures over a depth of 0·5 m. Standard error is indicated for mean elevation and fine sediment thickness; 95 % confident interval is indicated for surface grain size

| Type	Mean elevation above the low water table (m)	Fine sediment subsurface thickness (m)	Submersion duration (number of days per year)	Submersion frequency (number of submersions per year)	Surface grain size (mm) 10, 50 and 84 percentiles			Vertical subsurface profile
					D_{10}	D_{50}	D_{84}	
1	0·11 ± 0·11	0·05 ± 0·03	312	10·9	0·2 ± 0·03	1·2 ± 0·1	29 ± 32	
2	0·25 ± 0·09	0·04 ± 0·03	206	19·4	0·3 ± 0·04	1·3 ± 0·2	79 ± 53	
3	0·39 ± 0·10	0·02 ± 0·01	124	19·6	0·3 ± 0·06	2·0 ± 1·7	30 ± 27	
4	1·18 ± 0·37	0·01 ± 0·01	2·3	4·5	8·0 ± 4·00	50 ± 11·0	105 ± 23	
5	1·34 ± 0·19	0·37 ± 0·08	1·6	3·5	0·2 ± 0·01	1·1 ± 0·06	1·8 ± 0·1	
6	1·34 ± 0·20	0·39 ± 0·11	1·6	3·5	0·2 ± 0·01	1·0 ± 0·04	1·7 ± 0·1	
7	0·88 ± 0·50	0·23 ± 0·18	9·5	8·1	0·3 ± 0·02	2·0 ± 1·2	38 ± 50	
8	1·62 ± 0·18	>0·50	1·28	2·4	0·2 ± 0·00	0·2 ± 0·0	0·2 ± 0·0	
9	2·26 ± 0·38	>0·50	1·02	0·7	0·2 ± 0·00	0·2 ± 0·0	0·2 ± 0·0	
10	3·10 ± 0·29	>0·50	0	0	0·2 ± 0·00	0·2 ± 0·0	0·2 ± 0·0	
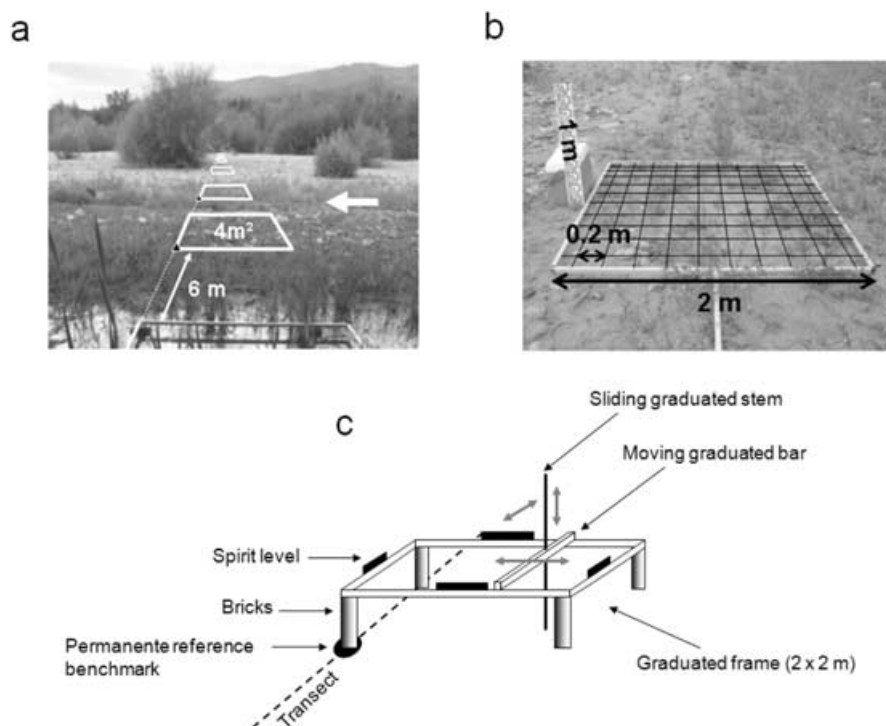
Figure 3. Sampling strategy: (a) representation of the sample transect on site 1. The white horizontal arrow indicates the flow direction; (b) oblique photograph of a 2 × 2 m plot. The sub-sampling zones of 0·2 × 0·2 m are indicated in the plot; (c) material and method for micro-topography measurements (explanations in the main text).

Backward and forward stepwise multiple linear regressions (with alpha-to-enter and alpha-to-remove = 0·05) were performed in order to identify and rank the hydrogeomorphic and biological independent variables explaining geomorphic changes. The plots impacted by a long distance drag effect were removed from this analysis in order to quantify only the local (immediate) effect of vegetation. Spatial and temporal floristic changes were estimated using the Bray–Curtis similarity index (Gower and Legendre, 1986) applied to vegetation abundance data.

The relation between seed bank structure and geomorphic dynamics was analysed using simple linear regressions. Comparisons between seed bank and vegetation used the Sorensen index (Gower and Legendre, 1986) applied to species absence/presence data. All statistical analyses were performed with SYSTAT™ v. 11, PRIMER™ v. 5 (Clarke and Gorley, 2001), and PAST™ v. 1·27 (Hammer *et al.*, 2001).

Results

Vegetation types and associated transverse gradient of diversity

In total, 442 plant species were identified in September 2002 on the two study sites, including approximately 25% exotic (alien) species. Mean Shannon diversity index (H') was 3·3 bits ± 0·3 SE. Mean species richness (s) per 2×2 m plot was 61·9 sp. ± 2·9 SE. 89·2% of the species were herbaceous plants; 7·9% were shrubs; and 2·9% were trees. Floristic differences among the ten vegetation types were significant (ANOSIM global test: $R = 0.93$, $P < 0.001$). The floristic composition of communities is given in Table II. Each vegetation type (Figure 4a, b) corresponded to one of the three structural groups that were expected to have distinct effects and responses during and between floods: group A: pioneer herbs and forbs (types 1 to 4); group B: pioneer shrubs and young trees (types 5 and 6); and group C: post-pioneer adult trees (types 7 to 10). Types 9 and 10 were not exposed to hydrogeomorphic disturbances during the study and so were excluded from analyses of change. Also, herbaceous types 2 and 3 were grouped into a single type 2/3 specifically for change analysis because of their physiognomic similarity and spatial proximity at the immediate margins of water channels.

Differences in diversity (H' and s indices) between vegetation types (Figure 5a, b) were also significant (one-way ANOVA for H': $F_{9,145} = 25·20$, $P < 0·0001$; for s: $F_{9,145} = 5·56$, $P < 0·0001$). A Tukey *post hoc* test indicated a decrease in mean Shannon diversity index (H') between the pioneer herbaceous/shrubby communities (types 1 to 6) and the post-pioneer forests (types 7 to 10). Species richness and mean Shannon diversity index reached their maximum values close to the main and flood channels in herbaceous types 2 and 3 (Figure 5a, b), where submersion frequency was the highest (Table IV). Proximity to the terrestrial zone (types 9 and 10) induced a significant increase in species richness (Figure 5a) related to annual herbaceous species of very low abundance mainly located within gaps in the riparian forest vegetation.

Overall biogeomorphic site dynamics

Mean net sediment deposition between 2002 and 2004 was + 0·18 m ± 0·29 SD at site 1 and + 0·15 m ± 0·20 SD at site 2, or respectively, 0·72 and 0·6 m³ per 2×2 m plot. Median sediment size (D_{50}) decreased by 3·1 mm ± 26·83 at site 1 (from 26·43 mm ± 24·25 SD in 2002 to 23·12 mm ± 31·18 in 2004) and 12·43 mm ± 31·28 on site 2 (from 22·20 mm ± 39·57 in 2002 to 9·77 mm ± 17·20 in 2004). This illustrated a tendency for fine sediment deposition.

Despite several significant floods exceeding bankfull (Figure 2), and net surface aggradation on both study sites, the percentage cover of herbaceous and woody strata in all 10 vegetation types remained the same between 2002 and 2004
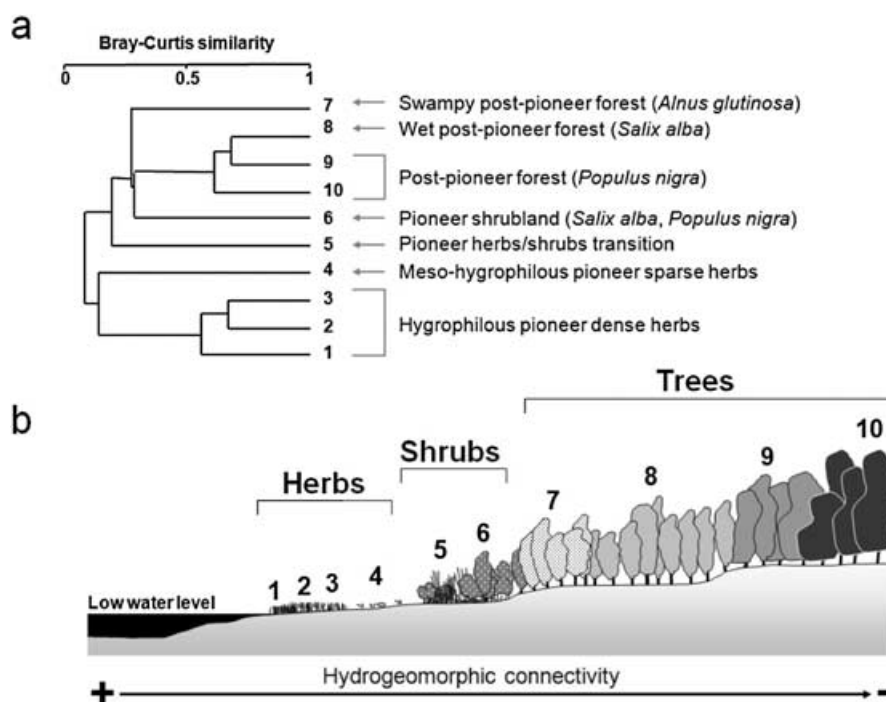

Figure 4. (a) Cluster dendrogram illustrating Bray-Curtis similarities between species composition recorded in the ten different vegetation types in 2002. (b) These types are represented schematically on the transverse gradient from the main water channel (on the left) to the floodplain (on the right).
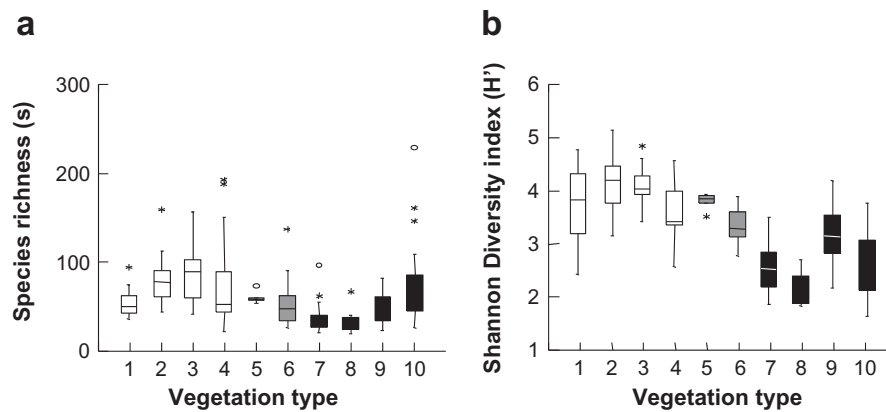
a

b

Figure 5. Vegetation type diversity: (a) species richness (s) corresponding to the number of species per 2 × 2 m plots. (b) Mean Shannon diversity index (*H'*) taking into account the number of individuals as well as number of taxa. The distributions are illustrated with box and whisker plots. The horizontal bar within each box represents the median, the lower and upper box limits represent the 25th and 75th percentile, and the whiskers extend to the 1st and 99th percentile. The circles represent the outliers, and the stars the extreme points. Group 1 (herbs and forbs) is represented in white; group 2 (shrubs and young trees) in grey; and group 3 (adult trees) in black.

Table V. Change analysis of ecological properties within vegetation types. Types 2 and 3 are treated as a single type (type 2/3) because of their spatial proximity. Standard error is indicated for all the variables. Results of repeated measures two-way ANOVA for diachronic evolution of ecological properties are indicated.

Type	Group	Mean herbaceous cover (% per 2 × 2 m)	Mean ligneous cover (% per 2 × 2 m)	Mean species richness	Mean Shannon Diversity index	Mean seedling cover (% per 2 × 2 m)	Mean seedling density of *Populus nigra* and *Salix* spp. (per 2 × 2 m)
2002							
1	A	81·75 ± 27·18	0·00 ± 0·00	3·20 ± 0·85	1·03 ± 0·37	3·17 ± 2·40	9·00 ± 6·36
2/3	A	63·67 ± 26·46	5·00 ± 13·42	10·14 ± 1·98	2·47 ± 0·30	33·25 ± 5·21	104·25 ± 26·15
4	A	1·05 ± 1·74	0·00 ± 0·00	1·25 ± 0·60	0·39 ± 0·20	1·89 ± 1·65	0·89 ± 0·65
5	B	66·00 ± 30·27	58·51 ± 37·51	7·00 ± 2·00	1·89 ± 0·00	7·00 ± 2·00	2·00 ± 0·00
6	B	15·89 ± 21·36	82·62 ± 34·55	3·67 ± 0·67	0·93 ± 0·31	0·00 ± 0·00	0·00 ± 0·00
7	C	15·40 ± 10·43	73·00 ± 41·31	6·50 ± 1·50	1·76 ± 0·05	0·00 ± 0·00	0·00 ± 0·00
8	C	22·75 ± 8·02	100·00 ± 0·00	6·49 ± 1·57	1·95 ± 0·35	0·00 ± 0·00	0·00 ± 0·00
2003							
1	A	96·25 ± 3·50	0·00 ± 0·00	4·33 ± 0·67	1·41 ± 0·35	6·33 ± 6·33	10·67 ± 10·67
2/3	A	75·23 ± 20·71	5·77 ± 20·80	7·86 ± 1·97	2·36 ± 0·26	26·50 ± 5·26	185·33 ± 62·50
4	A	10·62 ± 17·21	0·00 ± 0·00	2·78 ± 0·81	1·00 ± 0·34	1·22 ± 0·66	0·67 ± 0·33
5	B	73·25 ± 27·58	66·50 ± 26·30	7·50 ± 2·50	2·13 ± 0·00	3·50 ± 0·50	2·00 ± 1·00
6	B	25·37 ± 27·62	84·25 ± 34·81	7·00 ± 0·00	1·33 ± 0·35	0·00 ± 0·00	0·00 ± 0·00
7	C	17·86 ± 12·31	97·14 ± 7·56	5·00 ± 0·82	1·60 ± 0·14	0·00 ± 0·00	0·00 ± 0·00
8	C	25·00 ± 23·47	100·00 ± 0·00	8·00 ± 4·00	1·85 ± 0·71	0·00 ± 0·00	0·00 ± 0·00
2004							
1	A	86·12 ± 25·73	0·00 ± 0·00	5·00 ± 0·58	1·14 ± 0·55	6·60 ± 3·47	16·00 ± 8·20
2/3	A	75·00 ± 23·89	8·21 ± 24·60	9·38 ± 1·48	2·37 ± 0·18	35·60 ± 7·36	473·00 ± 82·46
4	A	5·55 ± 13·86	0·00 ± 0·00	2·38 ± 0·60	0·75 ± 0·23	0·87 ± 0·58	0·37 ± 0·26
5	B	55·00 ± 33·56	73·75 ± 23·93	7·50 ± 1·50	1·95 ± 0·12	1·00 ± 1·00	2·00 ± 2·00
6	B	26·12 ± 29·19	85·62 ± 34·99	8·00 ± 1·53	1·35 ± 0·18	0·25 ± 0·25	2·00 ± 2·83
7	C	21·82 ± 28·65	65·45 ± 44·80	5·50 ± 0·96	1·66 ± 0·11	0·20 ± 0·20	0·40 ± 0·40
8	C	23·50 ± 23·00	100·00 ± 0·00	7·00 ± 0·96	2·15 ± 0·25	0·00 ± 0·00	0·00 ± 0·00
ANOVA							
Type effect		$F_{7,178} = 58\cdot13$***	$F_{7,178} = 87\cdot64$***	$F_{6,71} = 11\cdot11$***	$F_{6,71} = 15\cdot19$***	$F_{6,71} = 26\cdot35$***	$F_{6,71} = 19\cdot30$***
Date		$F_{2,178} = 1\cdot84$	$F_{2,178} = 0\cdot56$	$F_{2,71} = 0\cdot54$	$F_{2,71} = 0\cdot52$	$F_{2,71} = 0\cdot08$	$F_{2,71} = 2\cdot17$
Type*date		$F_{14,178} = 0\cdot32$	$F_{14,178} = 0\cdot67$	$F_{12,71} = 0\cdot58$	$F_{12,71} = 0\cdot37$	$F_{12,71} = 0\cdot26$	$F_{12,71} = 4\cdot31$***

*** $P < 0\cdot0001$. Type effect: differences between vegetation types. Date effect: differences between dates; Type*date effect: differences between vegetation and dates.

(Table V). The species richness and mean Shannon diversity index (*s* and *H'*) also remained stable between September 2002 and 2004 at both sites (Table V). Change analysis of floristic composition within vegetation types, based on the relative abundance of plant species, also revealed significant overall stability. The mean Bray–Curtis similarity for each vegetation type was 0·72 ± 0·14 between September 2002 and 2003; 0·71 ± 0·16 between September 2003 and 2004; and 0·61 ± 0·25 between September 2002 and 2004 with an overall mean value of 0·68 ± 0·18. However, sediment accre-
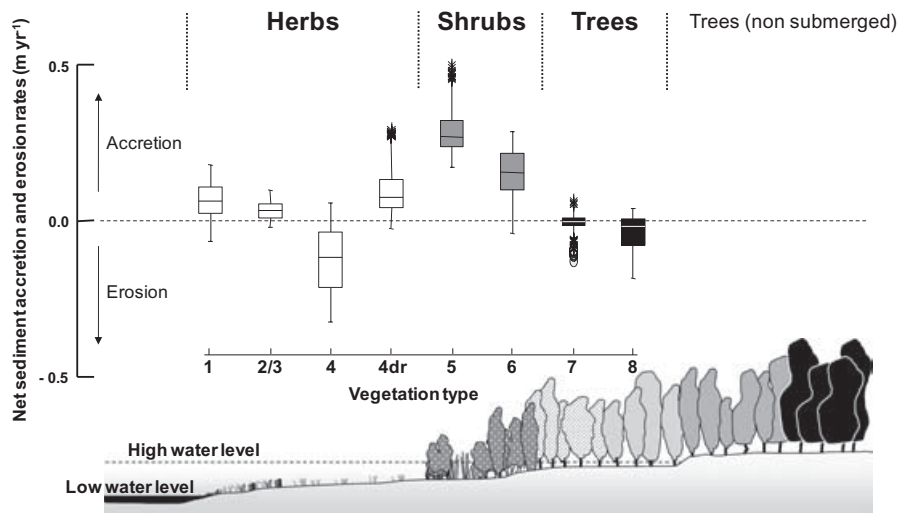
Figure 6. Mean net sediment accretion and erosion rates (m year^{-1}) recorded from 2002 to 2004 within vegetation types 1 to 8 which experienced hydrogeomorphic disturbances between 2002 and 2004. The distributions are illustrated with box and whisker plots (see Figure 5 for explanation). Group 1 (herbs and forbs) is represented in white; group 2 (shrubs and young trees) in grey; and group 3 (adult trees) in black.

tion intensity varied between vegetation types, in particular as clarified by a Tukey *post hoc* test between group B and the other two (Figure 6; repeated measures one-way ANOVA for the mean topographic variation between September 2002 and 2004, type effect: $F_{7,2392} = 997$, $P < 0.0001$). The mean Bray–Curtis similarity varied between 0.41 (type 5) and 0.91 (type 8), indicating that herbaceous types 1, 2/3, 4, and shrubby type 5 experienced low to medium floristic composition changes while riparian forest types 6, 7, and 8 experienced negligible changes.

Effects and responses of pioneer herbaceous types

Net sediment accretion rates within the herbaceous group (types 1, 2/3) was constant between September 2002 and 2004 (0.05 m year^{-1}, Figure 6), and fine calibre sediment (silt and sand) was continuously associated with this group. In close proximity to types 1 and 2/3 on the alluvial bars, type 4 with a very low vegetation density showed a clear tendency to flood scouring. Despite being located on the coarsest sediments (gravels, pebbles and cobbles, Table IV), all sampled type 4 plots that did not have any obstacle up stream recorded significant erosion (mean ~0.20 m year^{-1}, >0.5 m locally) between September 2002 and 2004. Erosion was only inhibited when upstream obstacles were present (type 4dr in Figure 6).

The floristic composition of the semi-aquatic type 1 remained very stable between September 2002, 2003 and 2004 (mean Bray–Curtis similarity between dates = 0.77), comprising the same abundant annual hygrophilous species (mainly: *Bidens frondosa, Cyperus eragrostis, Paspalum paspalodes, Polygonum lapathifolium, Typha latifolia*) (Table VI). Floristic changes observed in type 2/3 (mean Bray–Curtis similarity between dates = 0.59) at both sites were mainly a consequence of a random floristic recombination of more than 20 ephemeral meso-hygrophilous species among a pool of ~40 meso-hygrophilous annual, biannual or perennial herbaceous species of low abundance (Table VI). The permanent hygrophilous species systematically observed in type 2/3 were mainly *Bidens frondosa, Cyperus eragrostis, Echinocloa crus-galli,* *Lycopus europaeus, Lythrum salicaria, Paspalum paspalodes, Polygonum lapathifolium, Populus nigra* at juvenile stage, *Salix alba* at juvenile stage, *Xanthium strumarium.*

The permanently wet margins of channels between 0.10 to a maximum of 0.40 m above the low water level corresponding to the habitat for type 2/3, were also systematically heavily colonised by seedlings of *Populus nigra* and *Salix* spp. (Table V). This is reflected in the very significant statistical effect of vegetation type on *Populus nigra* and *Salix* spp. recruitment (Table V) and that, whilst this recruitment was constant within the extension area of type 2/3 (date effect not significant), mean seedling stem density showed significant variation among years (date × type effect). Nevertheless, mean coverage by juvenile *Salicacea* remained greater than 25% and mean seedling stem density was consistently higher than 100 stems per 4 m^2 (with a maximum of 473 in 2004) within type 2/3 sampling plots throughout the study (Table V). A significant percentage of the saplings persisted through the post-2002 floods, and so the mean height of juvenile *Salix* spp. and *Populus nigra* increased on both sites from 8 ± 6 SE (cm) in 2002 to 35 ± 23 SE in 2003 and 67 ± 75 SE in 2004. Thus, the Bray–Curtis similarity between the original 2/3 (herbaceous) type and type 6 (shrublands) increased significantly from 0.16 in 2002 to 0.46 in 2004, illustrating a tendency towards homogenisation of vegetation composition on alluvial bars as a result of rapid vegetation growth and a progression in succession.

Effects and responses of pioneer shrubland types

Alluvial bars colonised by pioneer woody communities experienced the highest mean sediment accretion rates (Figure 6). Mean annual accretion in types 5 and 6 between September 2002 and 2004 was greater than 0.20 m year^{-1} (Figure 6) in comparison with a mean net erosion of 0.20 m year^{-1} at a similar hydrogeomorphic disturbance level within type 4 (Figure 6).

Pioneer established trees resisted destruction, showing a mean growth rate of ~1 m year^{-1} within types 5 and 6 between 2002 and 2004. Floristic changes in type 5 resulted mainly from progression in the succession, according to the

Table VI. Presence/absence of plant species recorded for each vegetation type in 2002, 2003 and 2004. The numbers correspond to the occurrence on the three dates (1, 2 or 3 times). Numbers that are not in bold correspond to a surface cover ~ 1%; bold numbers correspond to a surface cover between 1 and 30%; bold and underlined numbers correspond to a surface cover greater than 30%.

Dominant species	Type 1	2/3	4	5	6	7	8
Acacia dealbata Link				**1**			
Agrostis stolonifera L.		3					**2**
Allium ampeloprasum L.					2		
Alnus glutinosa (L.) Gaert.		1				**_3_**	**_3_**
Amaranthus retroflexus L.		1					
Anagallis arvensis L.		1					
Angelica sylvestris L.							
Artemisia verlotiorum Lam.		1	1		3	1	
Artemisia vulgaris L.		1		1			
Artemisia campestris L.			2				
Arum italicum Mill.						1	1
Arundo donax L.						3	3
Bidens frondosa L.	**3**	**3**		1			2
Bidens subalternans D.C.		1					
Brachypodium sylvaticum (Huds.) P. Beauv.				3		2	1
Buddleja davidii Franchet	**1**						
Calystegia sepium (L.) R.B.		1		**_2_**			1
Carex sylvatica Huds.							1
Chelidonium majus L.						2	
Chenopodium album L.		2	2	**1**	3		
Chenopodium ambrosioides L.	1	1					
Chenopodium hybridum L.		1	1	**1**			
Chrysanthemum cegetum L.		1					
Conyza blakei Cabr.	1	1					
Conyza bonariensis (L.) Cronq.		1	1				
Cyperus eragrostis Lam.	**3**	**_3_**					1
Digitaria ischaemum (Schr.) Muhl.		**1**			1		
Digitaria sanguinalis (L.) Scop.		**1**					1
Echinocloa crus-galli (L.) Beauv.	**2**	3		1			
Epilobium hirsutum L.		1					
Fallopia japonica (Houtt.) Dcne.					**_3_**	3	2
Geranium robertianum L.					**1**		
Helianthus rigidus (Cass.) Desf.				**2**			
Humulus lupulus L.						**1**	
Impatiens balfourii Hook. f.				1	3	**3**	**3**
Juncus bufonius L.		2					
Lamium flexuosum Ten.						1	
Lamium purpureum L.		1					
Leersia orizoides (L.) Sw.	**1**	**2**					
Lunaria annua L.						1	
Lycopersicon esculentum Mill.		1			**1**		
Lycopus europaeus L.		2					
Lysimachia vulgaris L.		1					
Lythrum salicaria L.							1
Melilotus indicus (L.) All.		**2**	1	2			
Mentha suaveolens Ehrh.		3					
Nicotiana glauca R.C. Grah.							1
Oenothera suaveolens Desf.		1					
Panicum capillare L.		2					
Paspalum paspalodes (Mich.) Scrib.	**_3_**	3					1
Phalaris arundinacea L.	1					**_1_**	
Phytolacca americana L.				1	2		
Picris echioides L.		2					
Piptatpherum miliaceum (L.) Coss.							
Plantago lanceolata L.		1					
Plantago major L.		2					
Platanus × acerifolia (Ait.) Will.		1					
Polygonum lapathifolium (L.) Gray	**_3_**	**_3_**		**_3_**	3		
Populus nigra L.	1	**_3_**				3	3
Robinia pseudacacia L.	1	3	3	**_3_**	3		**_3_**
Rubus caesius L.						**_3_**	3
Salix alba L.	1	**_3_**		**_3_**	3	**_3_**	**_3_**
Salix eleagnos Scop.				**_3_**	3		3
Salix fragilis L.							3
Salix purpurea L.		3					3
Saponaria officinalis L.		1	**2**	**_2_**	1		
Senecio inaequidens DC.		1	1		1		
Setaria viridis (L.) P. Beauv.		2	2				
Sorghum halepense (L.) Pres.				**1**			
Trifolium pratense L.		1					
Trifolium repens L.		3					
Typha latifolia L.	3						
Urtica dioica L.				1	3	**_3_**	3
Xanthium strumarium D. Löve	1	**3**		**2**			

Bray–Curtis similarity between types 5 and 6 which increased significantly from 0·49 in September 2002 to 0·74 in September 2004. Net sediment deposition >0·5 m between 2002 and 2004 within type 5 (Figure 6) was accompanied by the loss in 2004 of three previously abundant hygrophilous herbaceous (*Bidens frondosa*, *Echinocloa crus-galli*, *Polygonum lapathifolium*) resulting in unit 5 being dominated in 2004 by *Robinia pseudoacacia*, *Salix eleagnos*, *Salix alba* and associated with less hygrophilous herbaceous species (mainly *Brachypodium sylvaticum*, *Calystegia sepium*, *Helianthus rigidus*, *Impatiens balfouri*, *Melilotus indicus*, *Saponaria officinalis*, *Urtica dioica*). Despite net sediment accretion >0·4 m, the floristic composition of pioneer woody type 6 remained stable between 2002 and 2004, dominated by *Salix alba* and nine resilient species (Table VI) well adapted to shade and a well drained sandy substrate.

Effects and responses of post-pioneer arboreous types

The topography of the less disturbed forested post-pioneer types (7 and 8) remained stable between 2002 and 2004 (Figure 6) with low average erosion rates (0·001 m yr^{-1}) reflecting very marked but localised regressive erosions. The topographically highest riparian post-pioneer forest types (9 and 10) were not flooded during the study and so were not monitored. Floristic composition of the swampy post-pioneer forest dominated by *Alnus glutinosa* (type 7) and the moist post-pioneer forest dominated by *Salix alba* (type 8) also remained

stable (mean Bray–Curtis similarity between the different dates: 0·91).

Effects of intercepted biovolume on sediment dynamics and seed bank structure

Intercepted biovolume explained 60 to 80% of sediment deposition monitored between 2002 and 2004. All other investigated independent variables were not significant or were of minor importance in comparison with the intercepted biovolume (Figure 7a–c, Table VII). Sediment accretion induced by vegetation was accompanied by the deposition of numerous diaspores. 17 090 diaspores (seeds and fruits) of 216 plant species including 29% exotic species were collected within the 148 bulk (10 cm^3) sediment samples. There were significant differences in seed bank structure between vegetation types (ANOVAs for species richness, $F_{7,138} = 22·01$, $P < 0·0001$; for seed abundance, $F_{7,138} = 23·25$, $P < 0·0001$), with three groups clearly distinguishable with the Turkey *post hoc* test (Figure 8a, b): (i) dense herbaceous types (1 and 2/3); (ii) the sparse herbaceous type 4; and (iii) the woody types (5 to 8). Dense herbaceous types exhibited an intermediate level of diversity with a high variability in seed abundance. Particularly high species richness and abundance (>50 species, >1200 seeds in 10 cm^3 sampled sediment) were found in some samples drawn from type 2/3, whereas others showed low species richness. The sparse herbaceous type showed very low seed abundance and diversity (<10 seeds and species per sample) while the woody types showed high values of
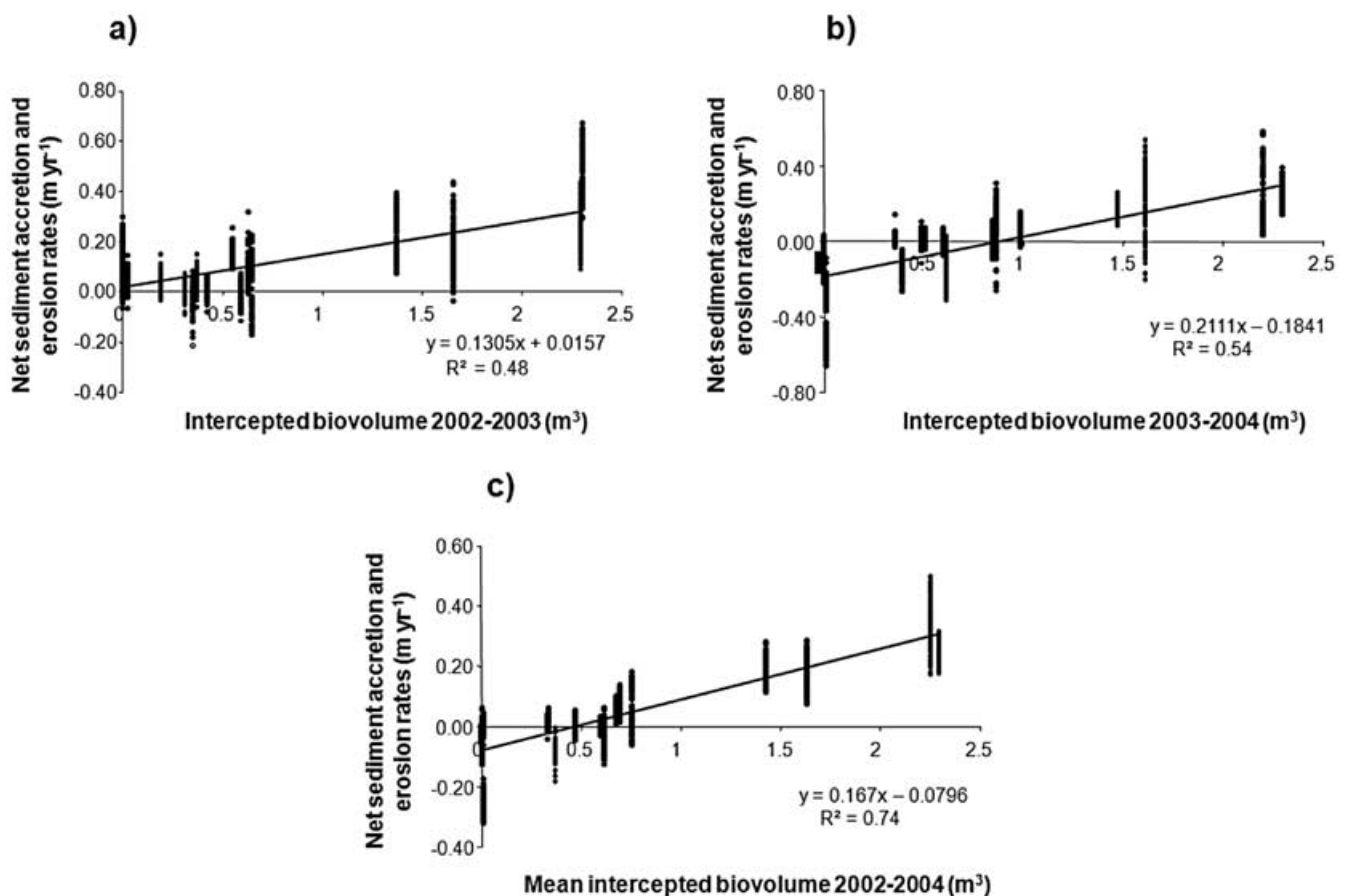

Figure 7. Linear regression models between the intercepted biovolume (independent × variable) and the net sediment accretion and erosion rates (m year^{-1}) (dependent y variable). The relations are positive and very significant. (a) 2002–2003: $F_{1,1698} = 1579$, $P < 0·0001$, $R^2 = 0·48$; (b) 2003–2004: $F_{1,1698} = 1984$, $P < 0·0001$, $R^2 = 0·54$; (c) Mean value (2002–2004): $F_{1,1698} = 4880$, $P < 0·0001$; $R^2 = 0·74$.

Table VII. Backward and forward stepwise multiple regressions with alpha-to-enter = 0·05 and alpha-to-remove = 0·05. The dependent variable is the net sediment accretion/erosion rate (m year^{-1}) within each sample quadrat that is not influenced by an upstream long distance drag effect ($N = 17$) between 2002–2003, 2003–2004 and 2002–2004.

| Variable	df	F	P	R²
2002–2003				
Intercepted biovolume	1	**30·3**	**<0·0001**	**0·73**
Surface sediment texture (D$_{50}$)	1	1·0	0·34	
Relative altitude	1	0·04	0·85	
Maximum flood height	1	0·67	0·43	
Mean flood height	1	0·67	0·43	
Distance to main channel	1	0·03	0·86	
Low strata mean cover	1	3·67	0·08	
Intermediate + high strata mean cover	1	0·56	0·47	
Low strata mean height	1	0·17	0·69	
Intermediate + high strata mean height	1	**7·44**	**0·016**	
Low strata mean stem diameter	1	2·64	0·13	
Intermediate + high strata mean stem diameter	1	2·88	0·11	
2003–2004				
Intercepted biovolume	1	**27·52**	**<0·0001**	**0·87**
Surface sediment texture (D$_{50}$)	1	**13·39**	**0·003**	
Relative altitude	1	0·003	0·96	
Maximum flood height	1	0·16	0·67	
Mean flood height	1	0·17	0·68	
Distance to main channel	1	0·15	0·70	
Low strata mean cover	1	0·20	0·66	
Intermediate + high strata mean cover	1	0·14	0·72	
Low strata mean height	1	0·54	0·47	
Intermediate + high strata mean height	1	1·20	0·29	
Low strata mean stem diameter	1	**5·47**	**0·036**	
Intermediate + high strata mean stem diameter	1	0·31	0·59	
Mean 2002–2004				
Intercepted biovolume	1	**62·13**	**<0·0001**	**0·80**
Surface sediment texture (D$_{50}$)	1	2·32	0·15	
Relative altitude	1	0·37	0·55	
Maximum flood height	1	0·32	0·58	
Mean flood height	1	0·31	0·59	
Distance to main channel	1	1·38	0·26	
Low strata mean cover	1	0·63	0·44	
Intermediate + high strata mean cover	1	0·006	0·94	
Low strata mean height	1	0·37	0·56	
Intermediate + high strata mean height	1	0·175	0·68	
Low strata mean stem diameter	1	0·47	0·50	
Intermediate + high strata mean stem diameter	1	0·008	0·93	
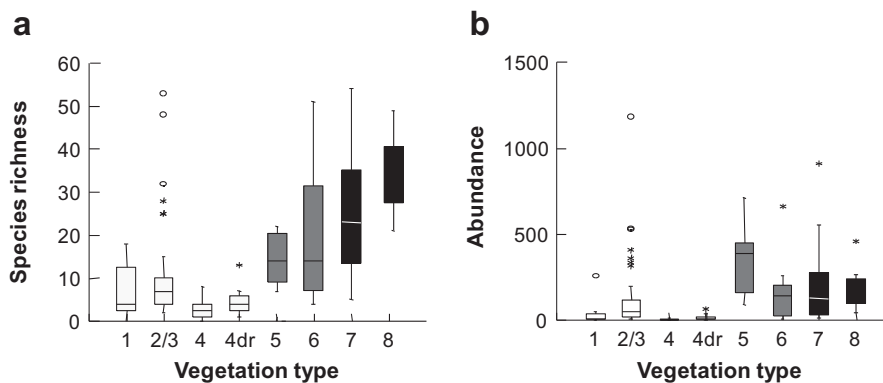
Figure 8. (a) Specific richness (number of species) of the seed bank and; (b) seed abundance (number of seeds) recorded within the monitored vegetation types 1 to 8 in 2002. Values in (a) and (b) are from 10 cm³ samples. The distributions are illustrated with box and whisker plots (see Figure 5 for explanation). Group 1 (herbs and forbs) is represented in white; group 2 (shrubs and young trees) in grey; and group 3 (adult trees) in black.
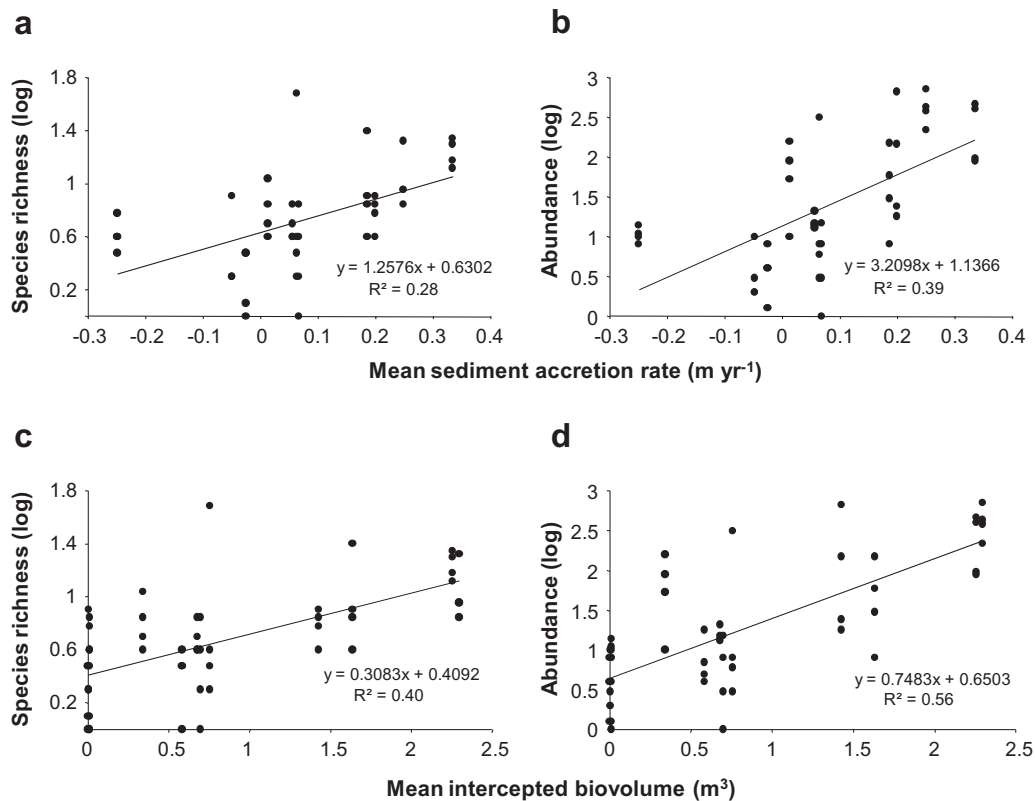
Figure 9. Linear regression models between: (a) mean sediment accretion rate (m year^{-1}) and species richness (log), $F_{1,42} = 13 \cdot 28$, $P < 0 \cdot 0001$; (b) mean sediment accretion rate (m year^{-1}) and seed abundance (log), $F_{1,42} = 26 \cdot 70$, $P < 0 \cdot 0001$; (c) mean intercepted biovolume (m^3) and species richness (log), $F_{1,50} = 33 \cdot 43$, $P < 0 \cdot 0001$; mean intercepted biovolume (m^3) and seed abundance, $F_{1,50} = 64 \cdot 85$, $P < 0 \cdot 0001$.

diversity and abundance and high intra-group variability. Seed banks within vegetation types 7 to 8 contained the highest species richness and seed abundance (Figure 8a, b). These post-pioneer forest types were not intensively submerged (mean water depth 0·1–0·3 m during 2002–2004 flood events), whereas vegetation types within the high flood frequency zone on the alluvial bars (types 1 to 6) were flooded to depths of 1 to 2 m.

Seed bank structure (species richness and seed abundance) and mean sediment erosion/accretion rates within the active tract (types 1 to 6) between 2002 and 2004 were significantly ($P < 0 \cdot 001$) and positively related (Figure 9a, b). Species richness and seed abundance were also significantly associated with the intercepted biovolume (Figure 9c, d). However, the R^2 values presented in Figure 9a–d ranged from 0·28 to 0·56, indicating a considerable amount of scatter in the regressions.

Overall, similarity in floristic composition between seed bank and standing vegetation within the different types was weak with the highest Sorensen similarity index found for type 2/3 (mean Sorensen similarity = 0·26 ± 0·05 SD; type 1 = 0·27; type 2/3 = 0·33; type 4 = 0·22; type 5 = 0·18; type 6 = 0·28; type 7 = 0·29; type 8 = 0·24).

Discussion

Vegetation control on sediment dynamics

The results indicate that annual variations in net sediment accretion rates along transverse gradients of the River Tech result from a complex combination of vegetative flow resistance and topographic position relative to the main channel.

Intercepted biovolume integrates several key hydraulic and vegetation properties that control local sediment accretion (Steiger *et al.*, 2005, 2007) and proved to be an effective surrogate for vegetation structure when exploring associations between vegetation and sedimentation in the present study.

Many studies have shown that sediment accretion decreases as tractive forces and sediment transport capacity decline from the main channel zone to the outer floodplain (Walling and He, 1998; Steiger *et al.*, 2001a, 2003). In parallel, sediment accretion generally decreases vertically with flood water depth. For example, Steiger *et al.* (2001b) defined a marked decrease in average 30-year sedimentation rates from 0·025 through 0·0067 to 0·005 m year^{-1}, respectively, between an abandoned side channel bed and margin to the forested floodplain of a site on the Garonne River, France, whereas Piégay (1995) showed that sediment accretion rates on the Ain River, France, were highest (0·04 to 0·08 m year^{-1}) on regularly inundated low floodplain surfaces densely colonised by pioneer vegetation, and were five to ten times lower on more elevated and less frequently (T 5–10 years) inundated surfaces. Similarly, Nanson and Beach (1977) found a decrease of sediment accretion rates along a transverse gradient across the Beatton River, Canada from 0·06 to 0·1 m year^{-1} on low surfaces colonised by pioneer vegetation within the active tract, to rates that were ten times lower on floodplain surfaces colonised by post-pioneer riparian forest. They suggested that vegetation density might interfere with this transverse pattern, explaining some of the variability observed between sampling locations. Our observations on the River Tech confirm the general tendency observed on transverse gradients across these other rivers, with a decrease of sediment accretion from 0·05–0·30 m year^{-1} close to the main channel to 0–0·01 m year^{-1} on the outer floodplain, but also, as suggested by

Nanson and Beach (1977) and more recently by Heppell *et al.* (2009), they show that vegetation structures induce very significant local variability in sedimentation rates (Figure 6).

Specific effects and responses of pioneer herbaceous types

Between 2002 and 2004, 0·10 m of fine sediment depth accumulated within dense herbaceous types 1 and 2/3 in the most exposed zones of the active tract of the River Tech, demonstrating that, in addition to the very effective erosion protection offered by roots and flattened vegetation canopy (biostabilisation), a dense herbaceous vegetation cover can also induce fine sediment trapping and retention (bioconstruction) (Elliot, 2000; James *et al.*, 2002; Righetti and Armanini, 2002; Samani and Kouwen, 2002). Similar processes have been observed within herbaceous structures on slopes (Prosser *et al.*, 1995) and in other river corridors (Steiger *et al.*, 2001a). The water depth of about 2 m can reasonably be assumed to have at least partly flattened submerged herbs during the floods experienced on the high-energy River Tech and this decrease in vegetation roughness within herbaceous types would explain the lower net sediment deposition rates (0·05 m year^{-1}) in comparison with semi-rigid shrubby vegetation types 5 and 6 (0·20 m year^{-1}) which were not fully submerged during floods.

Herbaceous types 1 and 2/3 were composed of different plant species with particular morphologies and biomechanics. Knowledge of the hydrodynamic behaviour of combinations of plants during river flood events remains, for practical reasons, very poor. Our results indicate the potential interest of performing complementary experimental research on the individual and combined controls of herbaceous species that may act as 'physical ecosystem engineers' on sediment dynamics *sensu* Jones *et al.* (1997). On the River Tech, such species could be *Bidens frondosa*, *Cyperus eragrostis*, *Echinocloa crus-galli*, *Paspalum paspalodes*, *Polygonum lapathifolium*, all of which were abundant during September throughout the study.

Floristic composition and surface cover of herbaceous types 1 and 2/3 were very resilient, remaining the same between sampling dates. The random recombination of low abundance ruderal species around a set of persistent species within type 2/3 explains the high plant diversity and density of herbaceous cover observed each September within the transition zone between water channels and alluvial bars on both study sites. Similar high diversities within pioneer herbaceous communities comparable with type 2/3 have been noted within diverse temperate riparian zones (Malanson, 1993; Naiman and Decamps, 1997; Tabacchi *et al.*, 1998, 2005; Gurnell *et al.*, 2006) and can be attributed to (i) the creation and maintenance of suitable habitat conditions for recruitment and settlement (fine sediment, access to water and nutrient resources), and (ii) to hydrogeomorphic disturbances which lead to increased diaspore diversity and abundance within the seed bank.

Our analysis of herbaceous group effects and responses to mean annual floods has demonstrated the narrow range in elevation (0 to 0·4 m max above low water level) within which vegetation types 1 and 2/3 exist in Mediterranean gravel beds. The herbaceous vegetation mosaic appeared to maintain similar plant communities and species, the same location relative to low water channels, and the same sediment-related functions of sediment and diaspore trapping and protection between years. As demonstrated by Tabacchi (1992) and Langlade and Décamps (1995), respectively on the Adour and

the Garonne Rivers, south-west France, the spatial distribution and extent of the herbaceous vegetation mosaic may change with subtle fluctuations (mm to cm) in the low water level, reflecting broader hydrological regime (drought, climate change) changes or direct human impacts (construction of weirs for water abstraction, gravel mining, hydrological regulation). Thus, subtle natural or anthropogenic hydrogeomorphic changes may lead to deep biogeomorphic changes because they determine the spatial distribution of engineering herbaceous communities that facilitate the recruitment of woody species within the active tract and on alluvial bars.

Specific effects and responses of pioneer shrubland types

The dynamics of erosion and deposition dominated by shrubs and young trees (group B, types 5 and 6, Figure 6) differed from the herbaceous group A, trapping much more sediment (0·20 m year^{-1} in comparison with 0·05 m year^{-1}), particularly sand, between September 2002 and 2004. In type 5 (combining herbaceous strata with dense shrubs) which also supported the largest biovolume, mean sediment accretion was particularly high (~ 0·30 m year^{-1}). Such enormous deposition of sand and finer sediment would not occur in the absence of vegetation roughness, as attested by observed erosion at the same elevation within type 4 and by increases in Darcy–Weisbach friction factor f with combinations of herbaceous and woody vegetation observed by Järvelä (2002) in experimental studies.

Pioneer ligneous species consistently resisted destruction during the observed floods and, consequently, floristic changes in transitional (between herbs and shrubs) type 5 were linked to a progression in plant succession with the growth of woody pioneer species (mainly *Salix* spp. and *Populus nigra*) and in type 6 to a tendency towards homogenisation of floristic composition. These progressions in the biogeomorphic succession under a mean annual flood disturbance regime, drives the system toward stability and post-pioneer stages. Types 7 and 8 (group C), which represent the next stage of the biogeomorphic succession at the study sites, remained stable with low sediment accretion rates, illustrating that water flows and sediment dynamics typical of a mean annual flood regime contribute to the successional process and that this will persist until an exceptional (high magnitude, low frequency) flood occurs that is sufficient to uproot post-pioneer trees.

Relations between biogeomorphic processes and seed bank structure

The strong dissimilarity recorded between the vegetation and seed bank on the River Tech suggests that diaspores are mainly imported from other sites by physical agents, although the dissimilarity probably does not have a single, unique cause, and confirms observations in other studies that, in general, riparian vegetation does not provide a good indicator of the quantity or species composition of diaspores within the seed bank (Goodson *et al.*, 2001; Tabacchi *et al.*, 2005; Gurnell *et al.*, 2008). For example, on the River Rhine, Germany, Beisman *et al.* (1996) concluded that the seed bank contained only 20% of the species present in the vegetation within the active tract; Deiller *et al.* (2001) showed that specific richness of the seed bank was weaker than the standing vegetation within the alluvial forest; and Hanlon *et al.* (1998) obtained similar results within riparian forests on the Alleghney Plateau, Pennsylvania, USA.

In the case of the River Tech, the dissimilarity between the vegetation and the seed bank can be attributed to some extent to species reproduction patterns. *Salix* spp. and *Populus nigra* produce very large quantities of short-lived seeds (no more than a few weeks, Karrenberg and Suter, 2003) and so these species are usually not represented in the seed bank. Some species reproduce mainly by vegetative processes (e.g. *Phalaris* spp.), while others, which are abundant within the River Tech seed bank (*Polygonum lapathifolium* and *Cyperus eragrostis* with, respectively, 6931 and 1650 seeds from the total of 17 090) characteristically produce very huge quantities of long-lived seeds. Second, physical agents, which transport (wind, animals, humans, and water flow) or mechanically disturb seeds (animals, humans, biological agents such as decomposition, predation) also have important effects on the seed bank (Fenner and Thompson, 2005).

The dispersal of diaspores is complex and still not well understood, but transport by water (hydrochory) has been identified by many authors as overriding other dispersal processes within fluvial corridors (Skoglund, 1990; Danvind and Nilsson, 1997; Andersson *et al.*, 2000; Goodson *et al.*, 2003). Sediment deposition by rivers is generally accompanied by massive deposition of seeds (Tabacchi *et al.*, 2005; Gurnell *et al.*, 2004, 2006, 2007, 2008) and our results suggest that the hydrological regime, the hydrogeomorphic exposure, and sediment erosion/deposition, which are strongly modulated by vegetation structures, are key controls on the structure of the seed bank along the River Tech.

Average seed bank similarity between different vegetation types on the River Tech was relatively high with low variance (Sorensen similarity: 0.67 ± 0.11 SD) in comparison with the similarity calculated for the vegetation (Sorensen similarity: 0.49 ± 0.15 SD), indicating homogenisation of species within the seed bank by water dispersal. Tabacchi *et al.* (2005) observed on the River Garonne, France, a significant increase in species richness within the seed bank near the river channel and an increasing similarity between the floristic composition of vegetation and seed bank with increasing distance from the river channel towards the floodplain, suggesting that hydrochory may induce spatial homogenisation of the seed bank within the active tract. However, Abernethy and Willby (1999) observed local tendencies towards increasing similarity between floristic composition of vegetation and seed bank adjacent to the main channels on colonisation sites. We also observed the strongest similarity (Sorenson similarity = 0.33) in type 2/3 very near to the main and the secondary water channels, suggesting maximisation of potential for germination under suitable conditions (available resources and recruitment sites) within this well connected aquatic-terrestrial ecotone (*sensu* Naiman and Décamps, 1997) where delivery of seeds by water is frequent and can be important (Figure 8a, b) and where the retention of fine sediments near the water resource favours vegetation development. The combination of suitable habitats for vegetation recruitment and good exposure to hydrogeomorphic fluxes and diaspore imports explains the high specific richness and diversity observed within type 2/3 (Figure 5a, b).

Positive, and statistically significant relations between mean accretion rates and seed species richness and abundance (Figure 9a, b) suggest the control of seed bank dynamics by hydrogeomorphic processes (sediment erosion and deposition) modulated by vegetation structure. Indeed, seed species richness and abundance were observed to be proportional to the mean quantity of sediment deposited between September 2002 and 2004 and were also correlated with intercepted biovolume (Figure 9c, d) where vegetation structures (types 1 to 6) were well exposed to water flow, reflecting the transverse

hydrogeomorphic gradient of exposure. The considerable amount of scatter in the regressions (Figure 9a–d) may be induced by several causes such as local variations in topography, hydrodynamics and variations in vegetation morphology and biomechanics. The interpretation of the effects of the combination of biophysical factors highlighted by the scatter plot, clearly requires analyses in experimental conditions.

Bornette *et al.* (1998) demonstrated on the River Rhône, France, that connected zones function as diaspore collectors while disconnected zones do not benefit from hydrochorous diaspore fluxes. Our results extend these observations, indicating a critical area between the well-connected active tract and the disconnected, high-elevation, rarely submerged floodplain. Although relatively weakly submerged during mean annual floods, the woody types 7 and 8 showed high seed diversity and abundance (Figure 8a-b). They also demonstrated weak floristic similarity between vegetation and seed banks (respectively 0·29 and 0·24), and relatively low species diversity in the standing vegetation (less than 50 species in types 7 and 8; Figure 5a) compared with the seed bank (around 80 species for 10 cm^3 in type 7 and 120 in type 8; Figure 8b).

From these observations, we suggest that diaspores in the seed bank were mainly imported by river flows, demonstrating inherent coupling between hydrogeomorphic dynamics and seed bank structure that does not simply reflect sediment processes but also that flotation and settling processes may play a decisive role on these relatively high flooded surfaces. Nilsson *et al.* (1991) and Johanson and Nilsson (1993) found similar surface segregation effects on Swedish rivers generating localised accumulations in particular zones according to seed flotation capacities. Stainforth and Cavers (1976) also showed that hydrodynamical factors (turbulence, water surface tension) can explain the mechanism of hydrochory. They found that certain seeds on the River Thames, Ontario, Canada (e.g. *Polygonum lapathifoluim*) are mostly transported on the water surface and tend to accumulate at the higher levels reached by floods. In the present study, significant quantities of *Polygonum lapathifolium* seeds were also found at relatively high levels within arboreous types 7 and 8, although this plant does not grow in this habitat, attesting to hydrochorous import of buoyant seeds.

Mechanisms that support deposition of diaspores within the active tract are complicated but, nevertheless, are significantly modulated by vegetation structures. Types 7 and 8 experienced low flow depths (around 0·2 m) during the observed floods but supported a dense, flow resistant vegetation cover capable of depressing flow velocities and allowing large quantities of buoyant seeds to be deposited. During the rising limb of floods, water spreading out from the low-flow channel, would have been able to mobilise seeds, particularly those that float. When flood waters reached their peak levels, they had probably collected significant quantities of seeds and those which remained floating were likely to have been deposited close to the peak flood level, within areas occupied by vegetation types 7 and 8. However, some seeds do not float and others lose their floating ability following extended contact with water. Middleton (1995) and Andersson *et al.* (2000) demonstrated experimentally that diaspores of different species spread through the water profile so that a combination of seed flotation and saltation probably drives sediment and diaspore deposition into vegetation structures during flood events. Deposition of floating seeds towards the end of floods probably occurs near obstacles at lower elevations, explaining the high diversity of both vegetation (Figure 5a, b) and seed bank (Figure 8a, b) within the herbaceous structures along the border of low-flow channels in types 1 and 2/3.

Biogeomorphic functions of pioneer herbaceous group A

A core aspect of our research was an investigation of the biogeomorphic function of herbaceous communities (types 1 and 2/3) in creating and maintaining suitable habitat conditions for themselves and other species. Facilitation is achieved by trapping diaspores and stabilising fine sediment within an area suitable for recruitment of many herbaceous species as well as *Salix* spp. and *Populus nigra* (see also Tabacchi, 1992 and Langlade and Décamps, 1995), but the precise role of pioneer riparian herbaceous plants as ecosystem engineers is poorly documented and identification of keystone or dominant species is still at an early stage.

Along the River Tech, few of the abundant species (e.g. *Bidens frondosa; Cyperus eragrostis; Paspalum paspalodes; Polygonum lapathifolium*) can be described as 'dominant' species which corresponds to abundant species that, as defined by Power *et al.* (1996) and Dayton (1972) 'define much of the structure of a community by creating locally stable conditions for other species, and by modulating and stabilising fundamental ecosystem processes'. Indeed, by facilitating recruitment of pioneer shrubs and trees, these abundant plant species appear to drive ecosystem structure and function responses to mean annual flood disturbances. On this high energy, gravel bed river, a dense herbaceous mat can create and maintain stable habitat conditions, promoting high species diversity and enhancing succession towards pioneer woody communities by sexual reproduction. As a result, massive recruitment of *Salix* spp. and *Populus nigra* (Table V) and high seedling growth rates (~ 60 cm between September 2002 and 2004) within the extension area of type 2/3 suggests that the progression in succession from type 2/3 towards type 6 could take place in a few years in the absence of severe droughts or exceptional floods (the Bray–Curtis similarity between vegetation types 2/3 and 6 increased from 0·16 in 2002 to 0·46 in 2004). At this recruitment stage, firm anchorage (biostabilisation) is fundamental to the spatial pattern of woody pioneer species, as was demonstrated by the high resistance of *Salix* spp. and *Populus nigra* seedlings that germinated in the study plots during 2002, and to prevent destruction by ensuing mean annual flood events.

There may be notable differences in survival between species and also between saplings and cuttings in these highly disturbed environments. For example, Karrenberg *et al.* (2003) investigated sapling growth and uprooting performance on the Tagliamento River, Italy, and found that *Salix elaeagnos* saplings had strong uprooting resistance, whereas *Populus nigra* saplings had inferior anchorage but superior growth rates under severe flood conditions. This may lead to greater success through vegetative reproduction. Since *Salix* spp. and *Populus* spp. recruitment is intimately controlled by hydrogeomorphic constraints (Mahoney and Rood, 1998; Cooper *et al.*, 1999; Johnson, 2000; Guilloy *et al.*, 2002), a rapid sequence of large floods, which can occur on the River Tech, could strongly modify the spatial pattern of ligneous species recruitment, favouring species capable of re-sprouting from vegetative fragments at relatively higher levels on alluvial bar surfaces (Francis, 2007).

Biogeomorphic function of pioneer shrubland group B

Salix spp. and *Populus nigra* showed strong resilience (success in recruitment) and mechanical resistance during mean annual disturbances. Following the facilitation effects of dense herba-ceous communities, *Salix* spp. and *Populus nigra* rapidly play a decisive role by regulating sediment transfer, and contributing to physical habitat and landform construction. These fundamental contributions to ecological succession allow pioneer woody species to be considered 'keystone' engineering species (*sensu* Paine, 1969) because they exert a disproportionate influence relative to their initial abundance. Their influences on riparian environmental parameters include sediment texture, hydrological connection, micro-climate (temperature and humidity) and access to light. As also observed on the River Tagliamento, Italy (Gurnell *et al.*, 2001, 2005; Gurnell and Petts, 2006), and on the Platte River, USA (Johnson, 1994), isolated woody plants (mainly *Salix* spp.; *Populus nigra*), initiate habitat and landform construction and associated ecological succession by creating accretion points for mineral and organic matter and by providing shade. In the absence of extreme floods, such accretion points can evolve rapidly, forming vegetated islands and extending floodplains within one or two decades (Zanoni *et al.*, 2008). A small group of individuals can be sufficient to induce a transition from disturbed pioneer stages with high levels of vegetation species richness characterised by annual and biennial ruderal species (*r* strategists *sensu* Grime, 1979) towards disconnected, stabilised post-pioneer stages with more complex food chains (Gurnell *et al.*, 2005).

Biogeomorphic function of post-pioneer arboreous group C

Strong species diversity and abundance were apparent in the seed bank within partly disconnected vegetation types 7 and 8, suggesting that less-disturbed riparian forests form a potential reservoir of vegetation diversity that could become immediately available to the fluvial corridor during large floods. Pioneer seed banks are well known to exhibit long-term viability (Thompson and Grime, 1979; Thompson *et al.*, 1993; Cavers, 1995; Fenner, 2000), but further research is needed to determine the viability of seeds stored in this river corridor reservoir of diversity and to quantify the hydrogeomorphic thresholds at which the reservoir may be tapped.

Positive feedback: the intermediate disturbance hypothesis revisited

Connell's (1978) intermediate disturbance hypothesis could be usefully extended by investigating the time required for feedback between biological diversity and hydrogeomorphic disturbance regime. In the corridor of the River Tech, the biogeomorphic shift from unstable pioneer stages with a high level of plant richness to post-pioneer stages exhibiting the lowest plant richness is driven by hydrogeomorphic disconnection, which is facilitated by pioneer types 1 and 2/3 but mainly controlled by transitional types 5 and 6. The decrease in plant diversity reflects the disappearance of several annual and biennial native or exotic herbaceous species and the persistence of more long-lived competitors, efficient in physically stabilised and disconnected habitats. This ecological succession, in the fluvial context, depends on the critical relationship between vegetation resistance and resilience and the hydrogeomorphic disturbance regime. Mean annual flood discharges (*T* 2–3 years), which were observed several times during the study period, are assumed to represent an optimum level for geomorphic change within channels and their immediate margins, through their impact on bedload transport
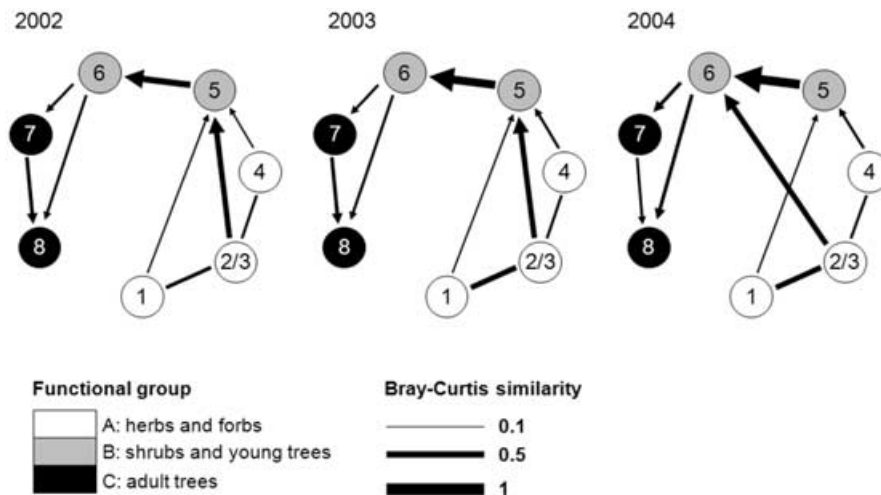
Figure 10. Bray–Curtis similarity between vegetation types in 2002, 2003 and 2004. The two larger values are represented for type 1 to 8 which experienced hydrogeomorphic disturbances between 2002 and 2004; the arrows indicate the direction of succession. Group 1 (herbs and forbs) is represented in white; group 2 (shrubs and young trees) in grey; and group 3 (adult trees) in black.

(Leopold *et al.*, 1964; Dury, 1976). However, significant progression of plant succession occurred, particularly in transitional types 2/3 and 5 (Figure 10), despite the occurrence of several such floods. The strong resilience of pioneer herbaceous labile species and the high mechanical resistance of shrubs and young trees (*Salix* spp. and *Populus nigra*), preserved the continuity in abiotic–biotic feedback through these mean annual disturbances, maintaining progression in the biogeomorphic succession.

Ecogeomorphic research has suggested that hydrogeomorphic and ecological processes and biodiversity in streams are inherently linked in a functional hierarchy (Schumm and Lichty, 1965, Naiman *et al.*, 1992, Van Coller *et al.*, 2000; Dixon *et al.*, 2002). The positive feedback observed on the River Tech provides an illustration of this, describing a bottom-up process of trapping and stabilisation of fine sediment by pioneer plants during mean annual floods determining the structure and function of the ecosystem at broader spatio-temporal scales. Corroborating observations made in other contexts (Nanson and Beach, 1977; Piégay, 1995; Walling and He, 1998; Gurnell *et al.*, 2001; Zanoni *et al.*, 2008), the biogeomorphic dynamics on the River Tech reflect a positive feedback between habitat and fluvial landform creation, construction, disconnection from hydrogeomorphic disturbances and stabilisation, that is initiated by herbaceous species and controlled largely by shrubby pioneer vegetation. As noted by Malanson (1993) and Bendix and Hupp (2000), such feedback may constitute a major driver of temperate fluvial ecosystem functioning, since it induces the characteristic shift from dominant geomorphic instability with high plant diversity to dominant geomorphic stability with lower biodiversity but higher productivity.

Despite differences in bioclimatic, hydrogeomorphic and anthropogenic factors, the underlying processes of the positive feedback may be similar across different regions. Different fluvial styles (e.g. single channel, meandering, island braided, braided, anastomosed) and dynamics (e.g. channel migration rates, island and floodplain growth rates) may reflect differential floristic, hydrogeomorphic, bioclimatic and anthropogenic contexts, rather than differences in the fundamental processes supporting the positive feedback. However, improved quantification of thresholds between resistive forces (sediment cohe-

sion and roughness modulated by plants) and destructive/regenerative forces (the flood regime) in different river systems are needed to investigate this theme further. Furthermore, our study based mainly on correlations indicates the interest to formally define the causal linkages between vegetation and sediment dynamics by *in situ* and laboratory experiments.

Concluding Remarks

This work has demonstrated the importance of herbaceous and ligneous pioneer vegetation in controlling geomorphic and ecological functioning at a local scale (on two alluvial bars and their margins over 3 years) and along a transverse gradient from the main low-flow river channel to the floodplain, of the River Tech, France. Three major functions of vegetation structure on biogeomorphic dynamics have been identified: (i) the facilitation function of the herbs and forbs functional group A, that is driven by fine sediment and diaspore retention in exposed zones of the active tract, and their positive effect on *Salix* spp. and *Populus nigra* recruitment; (ii) the function of the engineering shrub/pioneer tree group B on fluvial habitat and landform construction; (iii) the function of a 'diversity reservoir' within the post-pioneer group C, which can support ecological and landform regeneration after destructive floods. The extremely strong physical resistance of woody structures (shrubs and young trees) to flow and the strong compositional and functional resilience of labile herbaceous communities explain the positive feedback which occurs between exceptional flood events. Intermediate disturbances (mean annual floods: $T = 2–3$ years) lead, especially in the short term (a few years to a few decades), to the construction of stabilised habitats (i.e. islands, floodplains) and to the development of post-pioneer riparian forests.

The control (and the use) of flows of energy and matter, particularly sediment by vegetation structure, is a key component of ecosystem dynamics within fluvial corridors, which induces a biogeomorphic temporal sequence and a causal chain of habitat creation, maintenance and change. These functions carried out by pioneer herbs and shrubs have been established within the Mediterranean context of the River Tech. Further empirical field studies within different biocli-

matic contexts are now necessary. Specifically, the effects and responses of a combination of different vegetation types on sediment dynamics should be assessed in the field and by experiments according to different hydrogeomorphic, bioclimatic and anthropogenic contexts in order to define the range and varying nature of the effects and responses of vegetation. Furthermore, in order to define the limits in which vegetation–sediment feedback takes place, analysis needs to be conducted at regional scales including analysis of the effects of low frequency, high magnitude floods.

In conclusion, we stress the need to continue to develop the biogeomorphic approach and for geomorphologists to consider pioneer riparian vegetation as a fundamental dynamic control on physical morphogenesis and for hydroecologists to consider more explicitly the control of sediment dynamics by pioneer vegetation in river corridors as a key ecosystem function.

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