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Gudrun Bornette, Charles P Henriot, Florent Arthaud. Effects of a decennial spate flood on substrate and aquatic vegetation of riverine wetlands. *Aquatic Botany*, 2024, 194, pp.103789. 10.1016/j.aquabot.2024.103789 . hal-04661399

HAL Id: hal-04661399

<https://hal.inrae.fr/hal-04661399v1>

Submitted on 24 Jul 2024

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Effects of a decennial spate flood on substrate and aquatic vegetation of riverine wetlands

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ARTICLE INFO

Keywords:

Disturbance
Life-history traits
Nutrients
Resilience
Scouring

ABSTRACT

Spate floods control sediment, nutrient and biodiversity patterns in river floodplains, but the diachronic effects of spate floods on these compartments are rarely assessed. The effects of a 10-year flood spate on substrate characteristics and aquatic vegetation (community composition and life-history traits) were assessed before and after the spate in eleven former river channels that had become wetlands and varied in flood frequency. The effects of spate flooding on sediment and vegetation were expected to be greater in the less frequently flooded channels. For life-history traits, we expected a greater effect of the flood on tall evergreen species with high leaf area, while species with ruderal traits were expected to be less affected. For sediments, the flood reduced fine sediment cover and organic carbon content, but did not affect nutrient content. Vegetation cover decreased particularly in the most and least frequently flooded channels. Species richness and functional indices were little affected. The disturbance had a significant effect on plant traits, reducing tall evergreen species. This effect on plant characteristics increased as the frequency of overflow increased. The results highlight the key role of erosive floods in maintaining poorly competitive aquatic plants and limiting successional processes in riverine wetlands. Given the importance of plants in maintaining spate floodplain biodiversity, these erosive spate floods are essential to maintain or restore in a context of extreme river regulation.

1. Introduction

Along rivers, spate floods sculpt the relief of alluvial plains and govern the structure and dynamics of plant communities. The relationship between spate floods (either erosive or generating sediment deposits) and: 1) sediment in riverine wetlands (Schwarz et al., 1996) and 2) plant community composition (Bashforth et al., 2011) has been infrequently studied. In foothill rivers, spate floods generally last only a few days and have a high erosion potential, potentially stripping plant communities and fine sediment deposits (Fernandez et al., 2021). In contrast, lowland rivers generally have a low gradient and are considered a sink for suspended sediments (Sidorchuk, 2018) and nutrients (Schwarz et al., 1996)

Species richness and functional diversity of vegetation are unimodally related to spate flood intensity and frequency in a large number of studies (Santos et al., 2021), although the universality of these relationships is still under debate (Moi et al., 2020). In terms of plant species traits, high plant size and dry mass increase competitive ability

and are disfavoured by disturbance (Kautsky, 1988; Bornette and Puijalon, 2011b). Specific leaf area (SLA) tends to decrease (i.e. tissue density increase) in the event of disturbance (Louault et al., 2005). Finally, high root allocation (i.e. a high root/stem ratio) may confer greater resistance to uprooting (Schutten et al., 2005).

Of the studies dealing with plant life history traits in river spate floodplains (Catian et al., 2018; Ochs et al., 2020), very few concern aquatic vegetation, and most focus on plant dispersal (Thomason et al., 2018; Johnsen et al., 2021). Few studies have been published on other traits (Dalla Vecchia et al., 2020), and even fewer focus on the diachronically measured response to spate flooding (Chuman, 2008). Moreover, the response to erosion is generally measured indirectly, by linking plant characteristics to the frequency of disturbance (Bornette et al., 1994). Direct measurement of their effect on the substrate and plant communities is subject to the presence of a well-documented initial state (Henry et al., 1996), which is very rarely available.

The species traits that should be favoured by disturbance have been described (Grime, 2002), and some authors have proposed pools of traits

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<https://doi.org/10.1016/j.aquabot.2024.103789>

Received 30 January 2024; Received in revised form 13 June 2024; Accepted 17 June 2024

Available online 26 June 2024

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that should characterise aquatic habitats (Kautsky, 1988; Bornette and Puijalon, 2011b). Small species, characterised by great flexibility and strong anchorage, should be favoured in aquatic habitats subject to hydraulic disturbance. To date, to our knowledge, no publication has simultaneously measured the effect of a spate flood on sediments, plant communities and their functional traits in fluvial wetlands.

The aim was therefore to measure the effects of a ten-year winter spate flood on the aquatic vegetation and sediments of several former river channels located on the same spate floodplain and differing in the frequency of river overflow within them. The spate flood was expected to 1) erode sediments and leach nutrients, and 2) reduce plant cover and species richness, as well as functional richness, divergence and evenness. It was expected that the spate flood would have a more negative effect on tall species that are vegetatively present in the winter. In infrequently flooded channels, spate flood scouring is infrequent and consequently organic matter accumulation processes take place over longer periods between two spate flood events. Conversely, frequently flooded channels are frequently eroded and there may be little fine sediment available for erosion. As a consequence, the less frequently flooded channels were expected to be more eroded as they were not subject to recurrent

flood scour.

2. Material and methods

2.1. Study sites

The study was carried out on the Ain River in France (Fig. 1). The Ain is a tributary of the Rhône, located in the karstic context of the Jura mountains. It is a piedmont alpine river characterised by a coarse substrate (i.e. gravel, cobbles and sand). Seven natural channels abandoned by the river were studied. These channels are isolated from the river upstream by an alluvial plug and flow naturally towards the river downstream, with a flow that depends on the level of the water table. They all function as phreatic drains with slow or very slow flow velocities. During floods, the river can overflow these channels when it reaches the specific overflow rate for each channel. The current then rises sharply in the old channel, uprooting vegetation and washing away sediment. (Fig. 1). The abandoned channels studied differ in the minimum flow required for each of them to overflow (Table 1, Fig. 2). When the river is not overflowing, the channels are all apparently stagnant,

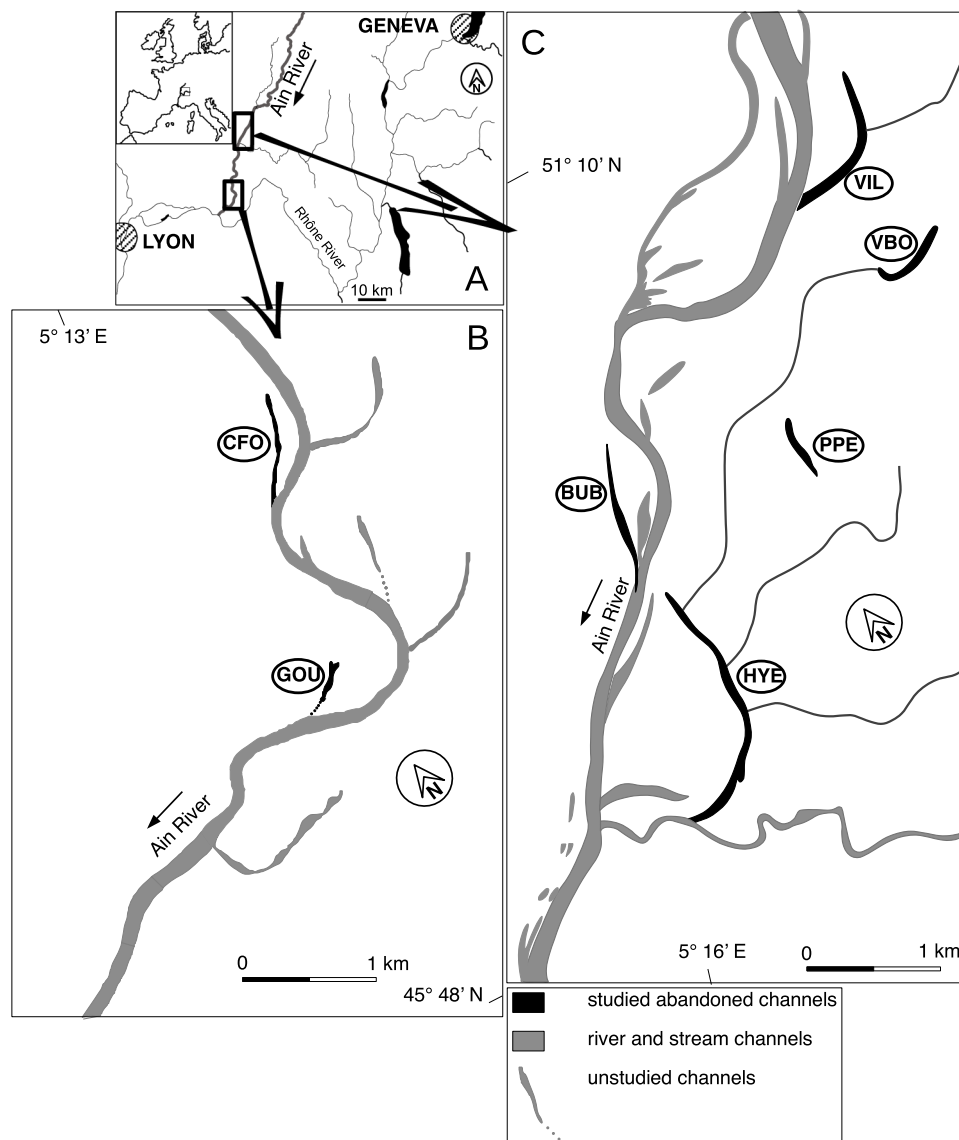


Fig. 1. Location of the study sites in the Ain River spate floodplain, France. (A) Location of the Ain River watershed in the upper Rhône watershed. (B) and (C) Location of the studied abandoned channels in the Ain River floodplain. The studied abandoned channels are darkened, in contrast to the Ain River and wetlands not covered by the study. Reference coordinate system: RGF93.

Table 1

Average physico-chemical characteristics of the sampled sediment cores expressed as average values \pm standard deviation per parameter, sampling date and cut-off channel. The number of cores sampled is indicated for one year of sampling (1998 or 1999), and the same transects were sampled for the two years. The key values of the t tests or Wilcoxon tests (depending on data normality) on paired data is indicated below and bolded if significant. The parameter abbreviation used in the text is indicated in the first column.

Channel	BUB	HYE	CFO	GOU	VIL	VBO	PPE	
average width (m)	15	9	6	11	8	14	9	
average depth (m)	1.3	0.68	0.81	0.54	0.58	0.27	0.06	
overflowing river discharge	130	350	400	850	950	1100	1100	
number of days of flooding by the river during the decade 1990–1999	1716	229	162	29	26	12	12	
number of cores sampled	6	5	5	5	6	8	5	
Parameter sampled	year of sampling and test values							
Organic C content (TOC %)	1998	3.2 \pm 0.7	6.04 \pm 2.41	4.04 \pm 1.15	6.67 \pm 1.16	6.33 \pm 1.48	9.74 \pm 9.16	10.66 \pm 3.56
	1999	1.9 \pm 0.37	2.72 \pm 2.64	2.67 \pm 0.29	5.22 \pm 3.05	5.54 \pm 1.33	7.39 \pm 4.31	8.36 \pm 1.76
	t value	4.0	2.5	2.9	1.4	0.97	0.75	1.1
Total C content (TC %)	1998	5.44 \pm 1.42	9.7 \pm 2.8	9.0 \pm 2.4	10.7 \pm 2.7	12.6 \pm 1.3	12.8 \pm 4.2	18.2 \pm 4.5
	1999	2.9 \pm 0.6	3.8 \pm 3.8	5.9 \pm 0.8	10.5 \pm 4.0	11.4 \pm 1.0	12.0 \pm 2.7	12.4 \pm 1.3
	Wilcoxon value	35	23	21	15	27	38.5	23
Kjeldahl N (N g.kg ⁻¹)	1998	1.8 \pm 0.6	3.1 \pm 1.6	2.1 \pm 1.1	3.3 \pm 1.9	4.08 \pm 1.0	6.6 \pm 5.3	7.1 \pm 2.7
	1999	1 \pm 0.4	1.1 \pm 1.5	1.5 \pm 0.5	2.9 \pm 2.8	3.4 \pm 1	4.4 \pm 3.9	5.6 \pm 1.1
	t value	2.4	2.4	1.1	0.5	0.9	0.9	0.9
fine substrate (%)	1998	67 \pm 25	78 \pm 26	71 \pm 43	99 \pm 2	88 \pm 13	90 \pm 28	100 \pm 0
	1999	31 \pm 15	30 \pm 23	42 \pm 53	99 \pm 2	83 \pm 40.8	85 \pm 23	100 \pm 0
	Wilcoxon value	4	2	8	12.5	22.5	22	12.5
Water content (%)	1998	52.0 \pm 14.5	62.2 \pm 11.3	56.5 \pm 12.3	64.3 \pm 12.5	76.6 \pm 4.2	77.5 \pm 15.8	73.5 \pm 2.2
	1999	51.2 \pm 8.1	49.8 \pm 22.2	47.3 \pm 8.9	57.2 \pm 19.0	77.6 \pm 8.0	74.7 \pm 7.8	65.3 \pm 5.2
	t value	0.05	0.96	1.37	0.60	-0.45	0.85	3.45
Total P (TP g.kg ⁻¹)	1998	0.73 \pm 0.19	0.50 \pm 0.12	0.62 \pm 0.13	0.58 \pm 0.19	0.55 \pm 0.05	0.55 \pm 0.23	0.64 \pm 0.22
	1999	0.60 \pm 0.15	0.38 \pm 0.19	0.48 \pm 0.05	0.56 \pm 0.24	0.55 \pm 0.08	0.55 \pm 0.22	0.66 \pm 0.21
	Wilcoxon value	26	18	21	13.5	19.5	31	11.5
	p value	0.22	0.29	0.060	0.92	0.86	0.96	0.92

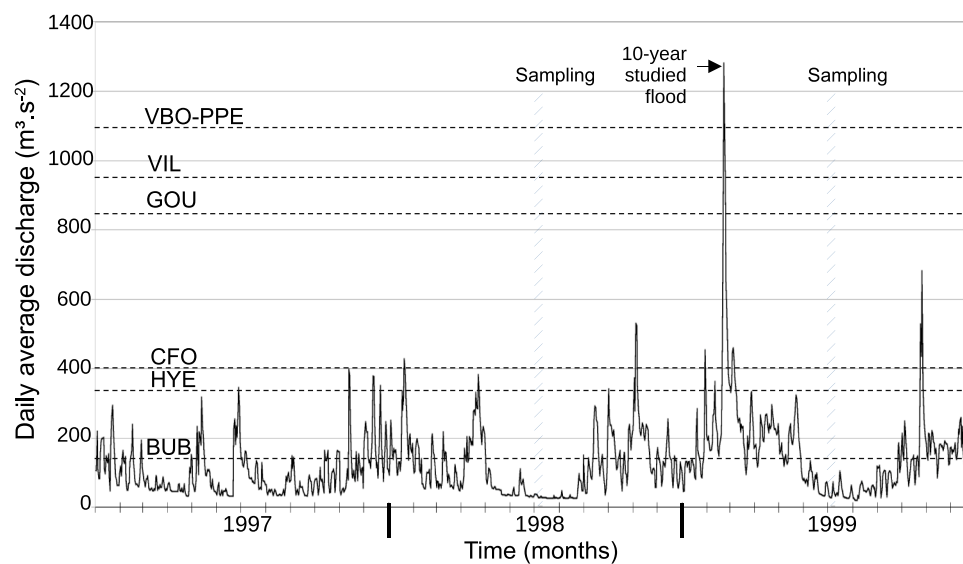


Fig. 2. Daily average discharge of the Ain River from January 1997 to December 1999 and minimum river flows required for each of the seven studied abandoned channels to overflow. The minimum river flows needed to overflow the seven studied abandoned channels are indicated by horizontal dashed lines. VBO and PPE had the same minimum overflowing level. The 10-year studied spate flood that overflowed the seven studied abandoned channels occurred in February 1999 (peak flow discharge 1281 m³.s⁻¹). The two sampling dates (*i.e.*, before and after the studied decennial spate flood, in July 1998 and July 1999, respectively) are indicated by two hatched bars.

except for the small riffles on HYE and CFO, where water velocities can reach 30–40 cm per second when groundwater discharge is high. The lower this minimum required flow is, the more frequently the river overflows the abandoned channel. The seven channels studied were overtopped by a 10-year flood in February 1999 (peak flow discharge 1281 m³.s⁻¹; Fig. 2). The overflowing discharge and number of

overflowing days over the decade (01/01/1990–31/12/1999) are indicated for each channel in Table 1. One of the cut-off channels (BUB) was overflowed a few months before the first survey (April 1998, peak river discharge 382 m³.s⁻¹). Two of them (HYE, and CFO), were overflowed during the previous winter (January 1998, discharge 429 m³.s⁻¹). Two others (VIL and GOU) were overflowed three years before

(July 1996, peak river discharge $950 \text{ m}^3 \cdot \text{s}^{-1}$). The last two abandoned channels (VBO and PPE) had not been overflowed for seven years (November 1992, peak river discharge $1120 \text{ m}^3 \cdot \text{s}^{-1}$; <https://www.hydro.eaufrance.fr/sitehydro/>).

2.2. Sediment characteristics

Sediment characteristics are indicative of dominant processes that operate in a river channel (*i.e.*, erosion vs. deposition). Fine substrate (*e.g.*, clay, silt) usually indicates silting processes and a low scouring effect (Wood and Armitage, 1999). Organic substrate indicates a low connectivity with the river allowing ecological succession to take place (*i.e.*, production and deposition of organic matter, (Rostan et al., 1987, 1997). Sediment aspect was surveyed before (*i.e.*, in July 1998) and after (*i.e.* in July 1999) the spate flood in the same set of 70 transects along the seven abandoned channels. Sampled plots consisted of 2 m-length strips. The width of the transects was determined by the abandoned channel width. Transects were regularly distributed along the upstream-downstream gradient of each channel (systematic sampling, 25–50 m between two sampling plots, four sampling plots from the smallest abandoned channel (*i.e.*, 250 m-length) to 20 plots for the longest one (*i.e.*, 750 m-length), respectively). The parts of the channels not being aquatic were not sampled. The proportion of coarse substrate occurring at the surface of the transect sediment (*e.g.*, sand, gravel, pebbles) vs. fine sediment, indicating either high or low scouring effect of spate floods, was assessed visually on each transect. We did not make a granulometric measure of the fine sediment grain-size. Indeed, a very significant part of the sediment is coarse in these channels (gravel, pebbles), and the granulometric measure can only be done on the finest part of the sediment (from silt to clay). As both are fine, and mineral, they were indirectly documented by the proportion of organic carbon, which inform on the organic part of fine sediment (Rostan et al., 1987).

Each time fine sediment occurred at the middle of the transect, sediment was sampled (*i.e.*, 40 plots sampled respectively in summer 1998 and 1999, 80 sediment samples in total). For this purpose, a sediment core sample was collected at the centre of the transect on both dates (*i.e.*, before and after the studied spate flood event, see Table 1 for the number of cores sampled for each channel at each date), and contents were measured in the upper five centimetres of sediment for each of the following: water, total organic carbon (TOC), total carbon (TC), total phosphorus (TP), and Kjeldahl nitrogen (N).

2.3. Vegetation sampling

Aquatic vegetation was surveyed before (*i.e.*, in July 1998) and after (*i.e.* in July 1999) the spate flood in the same set of 70 transects that were surveyed for sediment grain-size. The abundance of each species was estimated using the 5 cover classes of Braun-Blanquet (Braun-Blanquet, 1932). It was made possible by the good transparency and shallow depth of the water. Samples taken with a rake were reduced to a few individuals if a laboratory determination was necessary (*e.g.* Charophytes), but were avoided as much as possible to avoid destroying the population. The visual estimation of the relative cover of each plant species was made by the same person for the two sampling dates. Nomenclature followed Lambinon et al. (1992) and Corillion (1975) for Charophytes.

2.3.1. Indices of community changes

Species richness and cumulated plant cover were calculated at the transect scale, before and after the 10-year spate flood. For assessing functional changes in the plant communities, we used the Laliberté et al.'s functional indices, available in their R Package (Laliberté et al., 2014). The functional richness index (FRic) efficiently differentiates assembly rules regardless of species richness; the functional divergence index (FDiv) has the highest power value regardless of the assembly rule or the richness value; and the functional evenness index (FEve) is the

only one that allowed to consider simultaneously several life-history traits (Villeger et al., 2008).

2.3.2. Life-history traits

The life-history traits of aquatic species were documented. Rare species were not considered because the trait measurement would have been destructive. Species that occurred with an average abundance among sampling plots higher than 1 %, and that had a cover ≥ 50 % in at least one sampling plot, were documented. Destructive traits were measured on fully developed ramet individuals collected *in situ* in two wetlands independently from the present study, during the 1998 summer (in two groundwater fed channels located in the same area than the studied channels (Sous Bresse $45^{\circ}49'21.52''\text{N}$, $5^{\circ}14'25.45''\text{E}$; Méant $45^{\circ}48'7.03''\text{N}$, $5^{\circ}9'36.58''\text{E}$; the physico-chemical characteristics of the two channels are described in Bornette and Large (1995) and Bornette et al. (1998a). Sample size for plant traits was 34 ± 27 (mean \pm standard deviation) ramets per species.

Plant size (*i.e.*, aboveground plant height) was measured on fully developed ramets. Ramets were divided into roots (or rhizome + roots), stem, and leaf components. Dry masses of belowground and aboveground parts of the plants were determined from material dried at 70°C for 48 hours for calculating the root/shoot ratio. The leaf area was obtained before drying by scanning the fresh leaves of ramets on a flatbed scanner at 400 dpi. Projected leaf area was then measured using Vista scan and NIH Image 1.62. Photosynthetic area was measured for the whole ramet, and SLA was calculated as the ratio between the total leaf area of the ramet and the total leaf mass, in order to consider all the leaf types in case of heterophily.

All aquatic species occurring in the abandoned channels were perennial, but differed in their phenology, as some were evergreen and some summergreen. The evergreen character of the observed aquatic species was measured on 90 permanent quadrats (0.3×0.3 m) sampled in winter (*i.e.*, January 2000) and in summer (*i.e.*, July 2000). No spate flood occurred in the year before and between these two sampling dates in these channels. The percentage cover of each species was assessed and summed for each sampling date, providing a summer (SC) and a winter (WC) total cover value. The phenological index was then calculated for each species using the formula $1 + [(WC-SC)/(WC+SC)]$ and ranged between 0 (winter dormant species) and 2 (summer dormant species), a value of 1 indicating a species as abundant in winter as in summer (evergreen species).

2.4. Data analysis

2.4.1. Substrate

Depending on the normality and the homoscedasticity of the distribution of the parameter, we used either two-tailed t-tests of paired data or Wilcoxon tests, after Bonferonni's correction, to assess the changes in sediment characteristics before and after the flood (significance threshold $p=0.05$).

The changes in sediment physico-chemical parameters according to the overflowing thresholds of the different channels were analysed by linear and polynomial quadratic regressions. The overall significance test of multiple regression was associated to a Fisher-test value (F_{ddl} , residuals).

2.4.2. Indices of community changes

The changes in species richness, cumulated plant cover, and functional indices (*i.e.*, FRic, FDiv, and FEve) 1) along the gradient of overflowing thresholds of channels, 2) after the flood event, and 3) in response to the interaction between the flood event and the overflowing thresholds of channels, were analysed by linear and polynomial quadratic regressions. The overall significance test of multiple regression was associated to a Fisher-test value (F_{ddl} , residuals) whereas a Student-test value (t) was specified for specific explanatory variables in the global regression model.

2.4.3. Community changes in trait content

For each life-history trait and each channel, we calculated a trait value of the plant community before and after the flood. For this purpose, we did a co-inertia analysis, that links two tables: a plant trait dataset, containing the trait values of the 21 trait-documented species, and a plant abundance dataset containing the abundances of the 21 trait-documented species before and after the spate flood in all the transects of the seven channels. The plant abundance data set was first analysed through a within-class nPCA (Dos Santos and Thomaz, 2008), with each channel as a class, to focus on differences between the two sampling dates for the transects of a given channel. The plant trait dataset was analysed through a nPCA. Then, a co-inertia analysis was done to characterize the relationship between the change in species abundance between the two sampling dates and species traits (Bornette et al., 1994). The first axis of the co-inertia (49 % of inertia) was used to characterize, for each trait, the averaged trait value of the community in the transects for a given channel before and after the spate flood. The strength of the relationship was confirmed by the significant correlation between species abundance and traits for the two first axes ($\rho=0.8$, $p=9.10^{-4}$) and second axes ($\rho=0.8$, $p=3.10^{-4}$). Then, the average trait values of each channel before and after the spate flood were analysed according to the overflowing thresholds of the river in the channels by linear and polynomial quadratic regressions. The overall significance test of multiple regression was associated to a Fisher-test value ($F_{ddl, residuals}$) whereas a Student-test value (t) was specified for specific explanatory variables in the global regression model.

3. Results

3.1. Sediment characteristics

The sediment TOC, TC, N, and the proportion of fine substrate in the sediment of the most frequently overflowed channels decreased significantly after the spate flood (BUB, HYE; Table 1). In the third most frequently overflowed channel (CFO), only the sediment TOC decreased significantly (Table 1). The sediment characteristics did not change significantly in three overflowed channels (*i.e.*, GOU, VBO, and VIL). For one of the two less frequently overflowed channel (*i.e.*, PPE), the sediment total carbon content and water content decreased significantly. Sediment TP did not differ between the two sampling dates for each channel.

Sediment TOC, TC, N, and the proportion of fine sediment at the transect surface were positively correlated with the overflowing threshold of the channels and the strength of the relationships increased after the flood ($F_{5,74}=20$, $p=1.10^{-12}$; $F_{5,74}=36$, $p<2.10^{-16}$; $F_{5,74}=15$, $p=2.10^{-10}$; $F_{5,74}=11$, $p=9.10^{-8}$, respectively; Fig. 3). The water content of the sediment increased with the overflowing threshold, with no difference before or after the flood ($F_{5,74}=10$, $p=2.10^{-7}$). Sediment TP was not significantly linked to overflowing thresholds ($F_{5,74}=1.3$; $p=0.25$).

3.2. Changes in plant communities

Abundances of plant species (averaged by channel and sampling date) are listed in Appendix A. The species richness and plant cover decreased in all channels after the flood ($F_{5134}=4.5$, $p=9.10^{-4}$; $F_{5134}=3.6$, $p=4.10^{-3}$, respectively; Fig. 4). Before the flood, the species richness was lower at higher overflowing threshold, whereas the plant

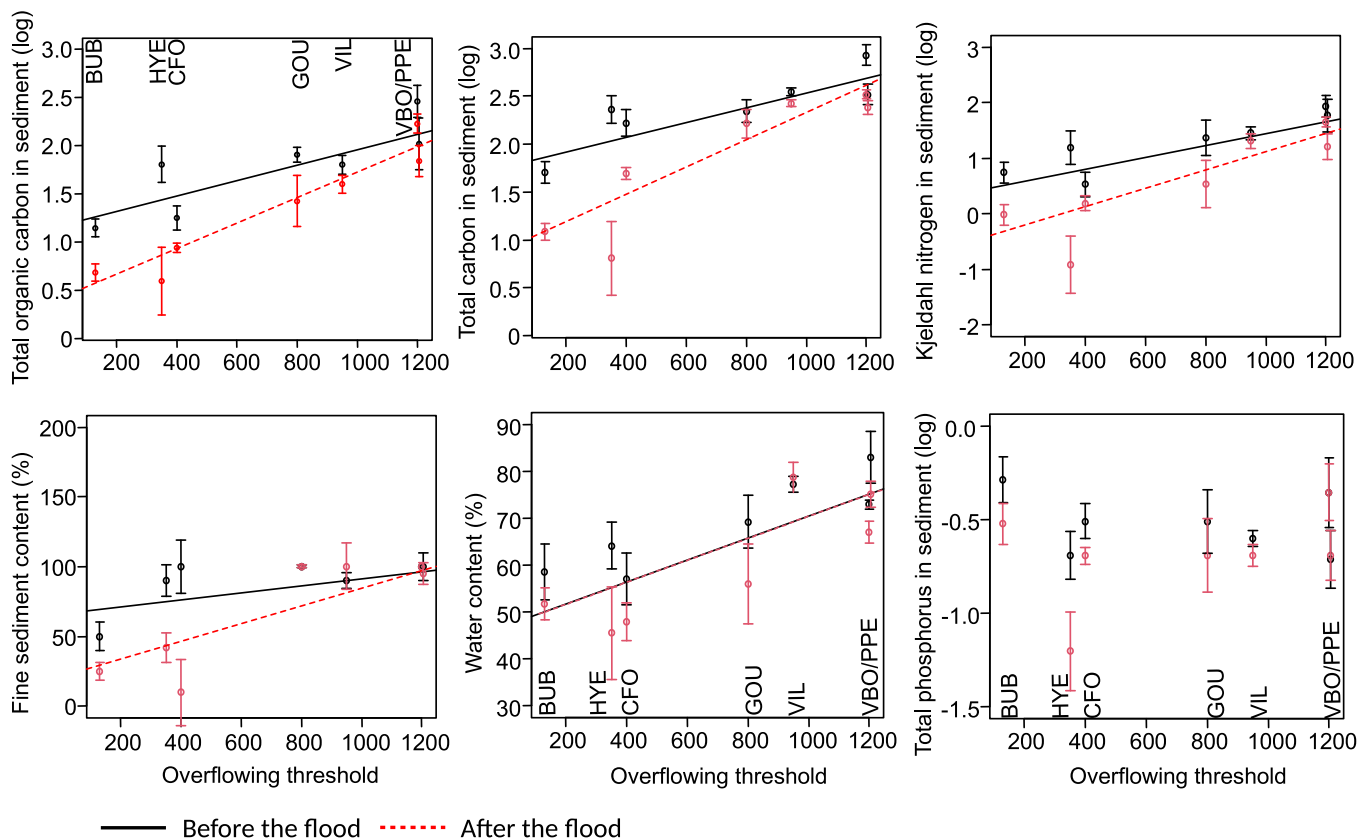


Fig. 3. Sediment characteristics of the seven studied abandoned channels, before and after the studied 10-year spate flood. Total organic carbon (TOC) concentration, total carbon (TC) concentration, Kjeldahl nitrogen (N) concentration, phosphorus (P) concentration, water content, and fine sediment content in the sediment of the seven studied abandoned channels. Silt and clay sediment were considered as fine sediment. TC, N, and P are logged-transformed. Measurements obtained before and after the 10-year studied spate flood are represented in black and red, respectively.

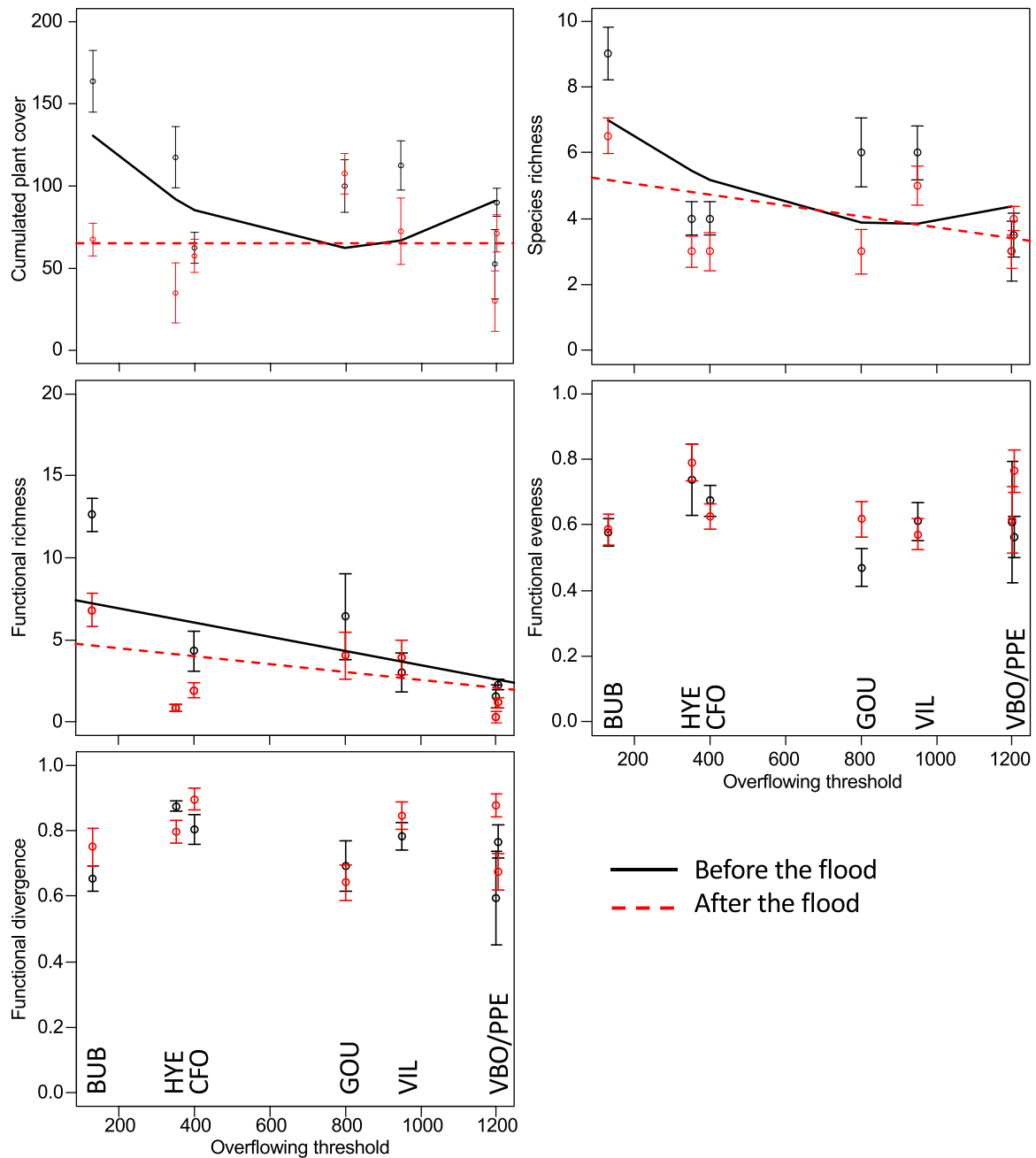


Fig. 4. Aquatic plant community indices according to the overflowing thresholds of the seven studied abandoned channels, before and after the studied 10-year spate flood. Cumulated plant cover, species richness, functional richness, functional evenness, and functional divergence of aquatic plant communities in the seven studied abandoned channels. Measurements obtained before and after the 10-year studied spate flood are represented in black and red, respectively.

cover had a unimodal relationship, with the highest values for both low and very high overflowing threshold ($t=-2.5$, $p=1.10^{-2}$; $t=2.7$, $p=7.10^{-3}$, respectively; Fig. 4). After the flood, the species richness was lower at higher overflowing threshold ($t=-2.5$, $p=1.10^{-2}$), whereas the plant cover did not vary along the overflowing threshold gradient ($t=0.5$, $p=0.6$).

Among the three functional indices, only the FRic was lower for higher overflowing threshold with no difference before or after the flood ($F_{3105}=5$, $p=2.10^{-3}$). FDiv and FEve were not significantly linked to overflowing thresholds and did not differ before and after the flood ($F_{3105}=0.7$, $p=0.5$; $F_{3105}=0.4$, $p=0.7$, respectively).

The variability of plant communities according to the within-class PCA was associated for 78 % to the floristic contrast between transects, while temporal changes (before-after flood) explained only 22 %

of the species variation. At the scale of the whole data set, the species whose abundance decreased the most after the flood were, in order, *Berula erecta*, *Ranunculus circinatus*, *Elodea canadensis*, *Juncus sub-nodulosus*, *Potamogeton coloratus*, and *Callitriche platycarpa*. The species whose abundance decreased the least after the spate flood were, in order, *Sparganium emersum*, *Elodea nuttallii*, and *Potamogeton natans*. In the two most frequently flooded channels, the flood mainly decreased the abundance of *Ranunculus circinatus*, *Elodea canadensis*, and *Sparganium emersum*. In the other five channels, *Sparganium emersum* was stable or increased slightly.

3.3. Changes in life-history traits

The trait values are listed in Appendix B. Before the flood, the plant

size and the anchorage depth were positively related to the channel overflowing threshold ($F_{3136}=4$, $p=8.10^{-3}$; $F_{5134}=4$, $p=2.10^{-3}$, respectively; Fig. 5). Both trends disappeared after the flood ($t=1.6$, $p=0.107$; $t=1.8$, $p=0.07$, respectively; Fig. 5).

The higher values of the root/shoot ratio of the communities were observed for the channels with an intermediate overflowing threshold before and after the studied flood ($F_{5134}=3.6$, $p=4.10^{-3}$; Fig. 5), and the relationship was not modified by the flood ($t=0.6$, $p=0.54$). The evergreenness of the plant communities was unimodally related to the abandoned channel overflowing threshold before the flood, the plant communities being more evergreen in abandoned channels with intermediate to high overflowing thresholds ($F_{5134}=3.8$, $p=3.10^{-3}$; Fig. 5). After the flood, the evergreenness index of the plant communities was more similar among the channels ($t=1.4$, $p=0.15$).

The average photosynthetic area of the plant communities did not vary significantly with the overflowing threshold of the channels but tended to increase after the flood for all the channels ($F_{1138}=3.8$, $p=0.09$; Fig. 5).

The SLA was negatively related to the channel overflowing thresholds ($F_{3136}=24$, $p=2.10^{-12}$; Fig. 5), and the relationship did not differ before and after the flood ($t=0.4$, $p=0.46$).

4. Discussion

4.1. Response of sediment characteristics to flood disturbance

We expected the flood to result in sediment and nutrient scouring. It was hypothesised that the effect of the flood would be greater in the less frequently flooded channels. This was based on the assumption that these channels had benefited from a longer period of sediment accumulation and vegetation growth (with species of higher biomass,

potentially more competitive). Probably due to the well-described 'flushing effect' of flood events (Pasquale et al., 2010), most sediment characteristics (i.e. TOC, TC, N and fine substrate sediment content) were positively correlated with the flood threshold gradient. After the flood, this relationship was strengthened, suggesting that this disturbance led to more efficient leaching of some of these nutrients and fine substrate in the most overflowed channels where the flood lasted longer. In fact, these channels were also those with the longest flow duration (i.e. about five days in the three most frequently overflowed channels, whereas the duration of the flood was shorter in the other channels: three days in the two abandoned channels with intermediate overflows and two days in the two least frequently overflowed channels). At the beginning of the flood, only the less elevated channels of the floodplain were flooded and the flow velocity was probably close to that of the river, especially when the sinuosity of the channels is low (Bornette et al., 1998b).

More surprisingly, the P content of the sediments was not related to the flood thresholds of the channels, contrary to what has been observed by other authors (Venterink et al., 2006). The rather low nutrient content of the river may explain this pattern: the low P-concentrated river water and sediment contribute little to the eutrophication of the riverine wetlands during floods.

The water content of the sediment increased with the channel overflow threshold, probably because it is related to the sediment organic matter content, which is higher in the less disturbed channels (Table 1 and Fig. 3).

4.2. Response of plant communities to flood disturbance

The most and least flooded channels tended to have higher pre-flood plant richness and cover. After the flood, as expected, species richness

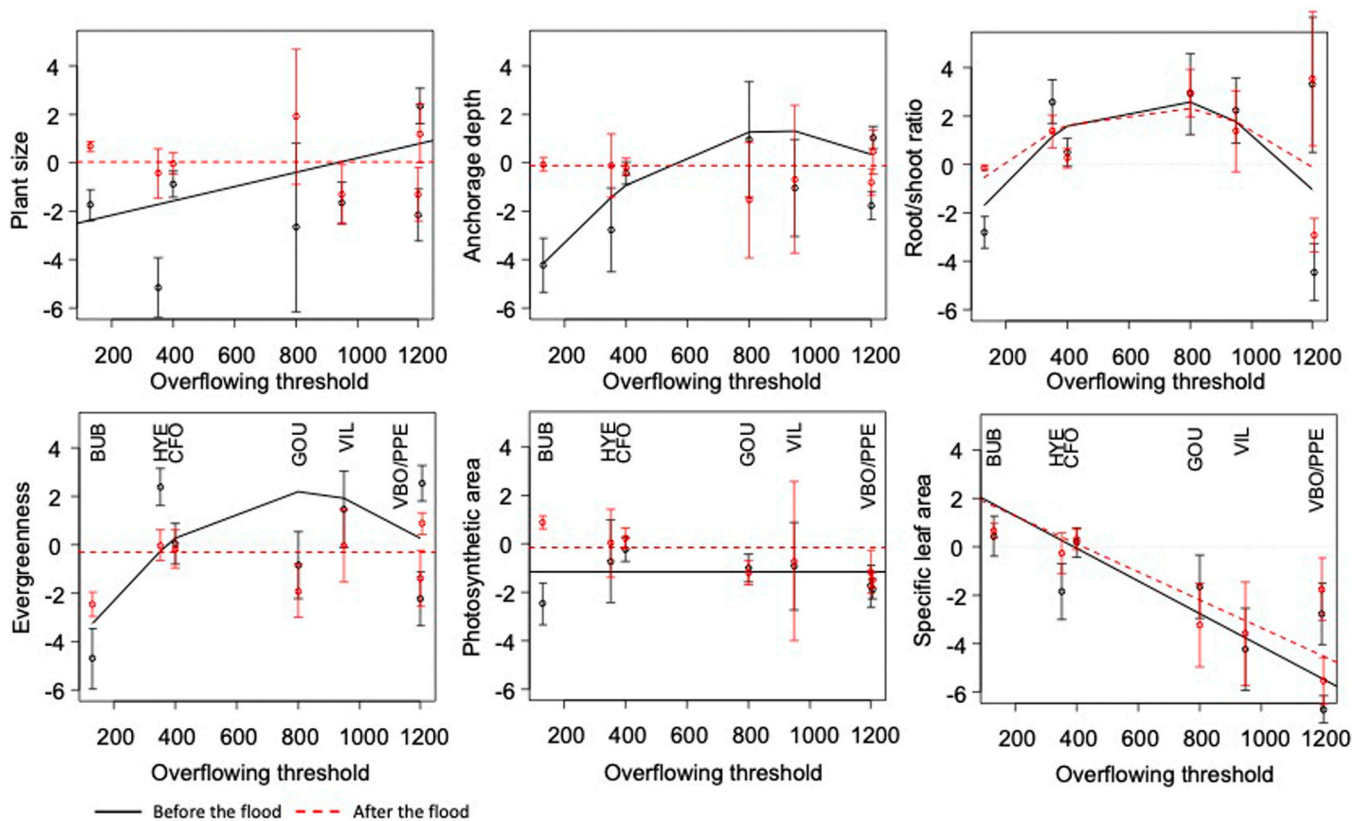


Fig. 5. Plant history-traits according to the overflowing thresholds of the seven studied abandoned channels, before and after the studied 10-year spate flood. Plant size, anchorage depth, root/shoot ratio, evergreenness, photosynthetic area, and specific leaf area of aquatic plants in the seven studied abandoned channels. Measurements obtained before and after the 10-year studied spate flood are represented in black and red, respectively.

and plant cover decreased in all channels, as previously reported (Henry and Amoros, 1996). According to the intermediate disturbance hypothesis, spate floods are expected to increase biodiversity in a unimodal manner, but this pattern is usually described by comparing sites subjected to contrasting flood regimes, rather than measuring the short-term effects of a specific spate flood event. The present study demonstrates that spate floods reduce plant cover and species richness in the short term. The unimodal disturbance-richness relationship was no longer observed after the disturbance, suggesting that the flood homogenised plant communities along the flood gradient. In frequently flooded channels, the greater destruction of plant communities may be related to the duration and severity of the disturbance, which affected 1) vegetative parts of plants that remained green during winter (Boyley and Sheldon, 1976), and 2) subterranean organs when sediment was scoured. Even species that were deeply anchored and dormant in winter, such as *Sparganium emersum* (i.e. rhizome depth of 6–10 cm in such habitats), decreased in abundance, suggesting that subterranean organs were at least partially scoured (Pollen-Bankhead et al., 2011). Flooding could also have introduced plant propagules into the channels, but the small changes in species content suggest that this input contributed little to the observed changes, in line with previous results (Cellot et al., 1998; Donath et al., 2003). In infrequently flooded channels, flooding reduced plant cover and species richness despite the lower duration of disturbance, suggesting a lower resistance of plant species to flood scouring in these habitats and/or a lower cohesive strength of the sediment (i.e. due to a high proportion of fine sediment), which favours plant uprooting (Bywater-Reyes et al., 2015).

The floristic contrast between channels was much higher than that between sampling dates (i.e., pre- and post-flood) because the flood disturbance gradient is superimposed on other ecological gradients, such as groundwater connectivity. In fact, the channels were fed by the oligotrophic hillslope aquifer (especially the less inundated channels) and the mesotrophic river seepage, contributing to the floristic contrast between them (Bornette et al., 2008; Mouw et al., 2009).

We expected a unimodal relationship between functional indices and flood thresholds according to the intermediate disturbance hypothesis, and a decrease in these indices after the flood. Instead, we observed that functional richness was negatively correlated with the frequency of channel overflow, with no effect of the flood, suggesting 1) that the gradient of channel overflow was not large enough to observe the unimodal relationship proposed by the intermediate disturbance hypothesis, and 2) that the studied flood had no effect on trait content and plant communities, regardless of the level of disturbance. Again, factors co-varying with the flood threshold could control functional diversity independently of the direct effect of the flood on plants. The proportion of seepage vs. hillslope groundwater in recharge depends on the elevation of the channel relative to the river (Bravard et al., 1997), and this could explain the variation in traits along the overflow gradient. The intensity and quality of groundwater supply control the degree of sediment oxidation and the trophy of the aquatic habitat, two parameters that strongly influence aquatic plants (Bornette and Puijalon, 2011a).

In terms of life-history traits, we expected a decrease in plant size due to erosion and a decrease in evergreen species due to the winter flooding. We also expected a greater effect of the flood in the less frequently flooded channels, because the longer delay between two disturbance events may have allowed the growth of species less resistant to disturbance. Before the flood, species tended to be taller, more evergreen, and more deeply rooted in the less frequently flooded channels, in line with the principle of size limitation in flood-disturbed habitats (Bornette et al., 2008; Violle et al., 2011). After the flood, this gradient disappeared. In infrequently flooded channels, the flood probably scoured some of the tallest and evergreen plants, leading to a homogenisation of plant size and a decrease in evergreen plants. According to Robertson et al., (2001), the timing of the disturbance appears to be a key factor determining the response of the plant community in abandoned channels: wintergreen plant species appear to be at a disadvantage during

winter floods. The persistence of evergreen and wintergreen species implies a trade-off between the risk of being flooded and the competitive advantage of being able to grow in winter (Boyley and Sheldon, 1976). Reduced seasonal temperature variability in groundwater-supplied wetlands (House et al., 2015) allows vegetation to grow throughout most of the year (i.e., including winter). In seasonally attenuated habitats, winter persistence would allow the use of temporal niches not normally available for plant growth, leading to better survival and recovery rates in the event of unpredictable disturbances (Adamec and Kučerová, 2013). The evergreen character, combined with the high regeneration potential of fragments, could also be considered as a trait increasing the resilience of aquatic species capable of producing and dispersing fragments during winter (Barrat-Segretain et al., 1999). Conversely, the evergreen character may also increase the sensitivity of plants and may not be a competitive advantage in cases of regular winter disturbance. However, it can be assumed that the hydraulic characteristics of plants vary to compensate for the increased risk of scouring due to winter persistence. For example, it has been shown that plant leaf area (probably involved in water velocity sensitivity) is controlled by the amount of light available (Ryser and Eek, 2000). During winter, shading from banks (deciduous trees) is reduced and plant cover in aquatic habitats (including plankton) decreases, providing better light conditions. This may consequently alter leaf size and structure at the within-species level, which unfortunately was not assessed in the present study. SLA and root/shoot ratio were not affected by flooding, but varied along the flood frequency gradient. SLA is usually positively related to disturbance tolerance, in agreement with our results (Macintyre et al., 1999; Weiher et al., 1999). The root/shoot ratio is driven by both the need to optimise anchorage strength and to store resources in nutrient-poor habitats: high flow velocity and nutrient limitation are correlated with higher root/shoot ratios (Carignan, 1982; Rattray et al., 1991). In the present study, frequently flooded channels tend to be richer in nutrients because they are mostly supplied by seepage from the river, which justifies their low root allocation. Infrequently flooded channels tend to be nutrient poor because they are supplied predominantly by hillslope groundwater, which is poorer in nutrients. In these channels the lower root/shoot ratio is more difficult to interpret. It may indeed be related to the low risk of uprooting, but one might expect these more oligotrophic species to allocate more biomass to roots to cope with nutrient stress.

Functional evenness and divergence were not correlated with flood frequency and were not significantly altered by the flood event. Given that the traits varied significantly along the flood gradient and between the two sampling dates, this raises questions about the ecological significance of these indices (Biswas and Mallik, 2010; Arthaud et al., 2012).

5. Conclusion

The present study has shown that spate floods are essential disturbances for the maintenance of habitat heterogeneity and biodiversity in piedmont and meso-oligotrophic piedmont floodplains. It has been shown that the ecological effects of a decadal spate flood affect both habitat characteristics and plant richness and traits. Contrary to what is usually observed, the studied flood did not lead to a nutrient enrichment of the sediments, but on the contrary to an export of fine substrate, carbon and nitrogen. From a successional point of view, the scouring flood has a clear effect on sediment deposition processes, slowing down sediment accumulation and competition processes in plant communities, and thus on ecological successions in riverine wetlands. In the context of oligo-mesotrophic rivers, spate floods appear to limit wetland eutrophication.

Spate floods tend to homogenise plant communities soon after their occurrence, and the contrasting hyporheic connectivity between abandoned channels is likely to be strongly involved in the floristic contrast along the disturbance gradient. In terms of traits, the flood mainly

affected large evergreen species, probably because they grew above the boundary layer and were vegetatively active during the winter flood. Further research on plant traits seems necessary to better understand plant resistance (e.g. hydraulic response to flow velocity, resistance to uprooting) and should assess the variability of such traits during the annual cycle. Seasonal variation in plant traits may also provide important insights into how plants cope with seasonal variability in such habitats.

The most frequently flooded channels were more affected by the decadal flood in both sediment and plant community characteristics, suggesting that frequently flooded channels may have experienced higher flow velocities and longer duration of the disturbance event. Frequency of flooding is unlikely to be sufficient to accurately describe the erosive power of flood events. Flow volume and velocity could probably lead to a better understanding of these processes, but are unfortunately very difficult to measure or model in riverine wetlands.

This study outlines, at a local scale, the key role of erosive spate floods in maintaining aquatic plant communities and limiting successional processes in alluvial wetlands. Given the critical importance of plants in maintaining aquatic biodiversity, these erosive processes are particularly important in the context of extremely high levels of regulation of large rivers, leading to the complete cessation of river mobility and the fossilization of fluvial forms. The dramatic impoverishment of aquatic communities along large rivers is related to the collapse of floodplain habitat diversity, which is strongly associated with river regulation (Aarts et al., 2004). The need to compensate for changes in river dynamics is a key issue and needs to be considered more systematically in river floodplain management. This is essential before entire

biodiversity compartments in alluvial valleys disappear, and this cannot be solved simply by local wetland restoration. Indeed, such restorations, which usually consist of sediment removal, are often unsustainable as they do not affect the key fluvial processes that maintain biodiversity in these hydrosystems (Guerrin, 2015).

CRediT authorship contribution statement

Florent Arthaud: Writing – review & editing, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Charles Henriot:** Writing – review & editing, Validation, Conceptualization. **Gudrun Bornette:** Writing – original draft, Methodology, Investigation, Funding acquisition.

Declaration of Competing Interest

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

Data Availability

Data will be made available on request.

Acknowledgments

The study was supported by the National Centre for Scientific Research, France.

Appendix A. Average cover percentage of aquatic plant species before (98: July 1998) and after (99: July 1999) the flood in the cut-off channels under study

	BUB		CFO		GOU		HYE		PPE		VBO		VIL	
Sampling date	98	99	98	99	98	99	98	99	98	99	98	99	98	99
Channel length (m)	350		750		300		450		250		525		225	
Number of sampling plots	10		20		7		9		4		10		9	
<i>Baldellia ranunculoides</i>									17					
<i>Berula erecta</i>			19	15	49	29	71				17		38	22
<i>Callitriche platycarpa</i>	28	8	18	14	6	3	7	49					4	
<i>Ceratophyllum demersum</i>	2	2		8				7						
<i>Chara major</i>					2	9					2		11	13
<i>Chara vulgaris</i>									1				12	
<i>Elodea canadensis</i>	52	18	11	10	6		4							
<i>Elodea nuttallii</i>	42	36	6	16			2	2					2	
<i>Fontinalis antypiretica</i>			2											
<i>Galium palustre</i>			16	6	17	9			7				7	2
<i>Glyceria fluitans</i>						3					2			
<i>Groenlandia densa</i>	8		3	2	9								9	11
<i>Hippuris vulgaris</i>				2	14	9	9						13	22
<i>Hottonia palustris</i>			3		6			9						
<i>Juncus articulatus</i>			8		17	17			27		1		29	36
										27		8		

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	BUB		CFO		GOU		HYE		PPE		VBO		VIL	
<i>Juncus subnodulosus</i>									3		76		27	16
<i>Lemna minor</i>				16						3			6	
<i>Lemna trisulca</i>			15	5										
<i>Mentha aquatica</i>	6	4	3	8	2	31	38		23		22		18	24
<i>Myosotis scorpioides</i>	1	8	3	6	6	17	7		29		17		24	7
<i>Myriophyllum spicatum</i>	12	6	16	8	11				9					13
<i>M. verticillatum</i>				3		6			2					7
<i>Nasturtium officinale</i>	2		8	8							6			
<i>Nitella opaca</i>	8													
<i>Nuphar lutea</i>	28	4	2		3	3								
<i>Oenanthe fistulosa</i>							24							
<i>Potamogeton coloratus</i>							11		22		14		36	22
<i>Potamogeton natans</i>	12	12	2	16	34	31			2		2		18	7
<i>Potamogeton pectinatus</i>		2											14	16
<i>Potamogeton perfoliatus</i>	2	4	8											
<i>Potamogeton pusillus</i>	8	4	4	5	5									
<i>Ranunculus circinatus</i>	48	4	8	2										
<i>Ranunculus trich. x circi.</i>				8					3					
<i>Ranunculus trichophyllus</i>					6									
<i>Rorippa amphibia</i>			16		6	9								
<i>Sagittaria sagittifolia</i>	22	22	5.6	4.8										
<i>Samolus valerandi</i>									3.4		14			
<i>Sparganium emersum</i>	52	36	23	30	23	23	13						16	
<i>Sparganium minimum</i>								27	17					
<i>Utricularia sp.</i>									3		7			
<i>Veronica a.-aquatica</i>	2		6											
<i>Veronica beccabunga</i>			16											
<i>Zannichellia palustris</i>				2										2

Appendix B. : average values of life-history traits measured on the 21 submerged species studied. N: number of ramets sampled; height of the ramet (cm), SLA: specific leaf area ($\text{cm}^2 \cdot \text{g}^{-1}$), root/shoot (below-ground/above-ground dry mass), ramet photosynthetic area (cm^2), evergreenness (for the calculation of the index, see the method section), rooting depth (cm)

Species	N	height	photosynthetic area	SLA	root/shoot ratio	evergreenness	Rooting depth
<i>Baldellia ranunculoides</i>	62	30.8	154.0	368	.518	1.8	14.0
<i>Berula erecta</i>	95	19.3	38.6	485	.556	1.0	9.5
<i>Callitriche platycarpa</i>	31	25.0	7.0	1045	.257	1.0	12.1
<i>Ceratophyllum demersum</i>	18	89.7	14.7	24	.000	.7	0.0
<i>Elodea canadensis</i>	17	37.6	41.9	836	.392	1.0	18.5
<i>Elodea nuttallii</i>	21	25.0	24.9	904	.142	.8	9.6
<i>Groenlandia densa</i>	58	25.4	17.2	981	.154	.9	7.5
<i>Hippuris vulgaris</i>	11	50.2	284.6	939	.224	1.1	14.9
<i>Juncus articulatus</i>	24	18.5	6.3	123	.943	.5	13.0
<i>Juncus subnodulosus</i>	15	63.5	45.8	86	.091	1	14.7

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Species	N	height	photosynthetic area	SLA	root/shoot ratio	evergreenness	Rooting depth
<i>Lemna trisluca</i>	6	2.7	0.3	961	.000	.9	0.9
<i>Mentha aquatica</i>	90	27.8	36.4	385	.258	.6	11.9
<i>Myriophyllum spicatum</i>	9	80.8	95.8	852	.421	1	19.7
<i>Myosotis scorpioides</i>	69	14.8	32.4	421	.702	1.2	14.6
<i>Nasturtium officinale</i>	9	79.5	101.1	719	.172	1.6	30.6
<i>Nuphar lutea</i>	20	109.0	1149.8	113	.189	0.1	78.0
<i>Potamogeton coloratus</i>	62	44.0	133.0	520	.124	0.7	9.0
<i>Potamogeton natans</i>	41	105.7	81.8	196	.173	0.7	13.2
<i>Sagittaria sagittifolia</i>	23	34.3	90.5	573	.459	0	11.0
<i>Samolus valerandi</i>	18	11.8	71.4	525	.280	.7	13.1
<i>Sparganium emersum</i>	22	64.7	121.2	572	.347	.2	12.1

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