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Sabine Greulich, Richard Chevalier, Marc Villar. Soil seed banks in the floodplain of a large river: A test of hypotheses on seed bank composition in relation to flooding and established vegetation. *Journal of Vegetation Science*, 2019, 30 (4), pp.732-745. <10.1111/jvs.12762>. <halshs-02455661>

**HAL Id: halshs-02455661**

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Submitted on 31 Oct 2025

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## Soil seed banks in the floodplain of a large river: a test of hypotheses on seed bank composition in relation to flooding and established vegetation

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### Abstract

**Questions:** This study investigates soil seed banks in relation to established vegetation in the floodplain of a large river with high energy floods. It addresses the composition of seed banks and extant vegetation over a wide flooding and succession gradient. Tested hypotheses were: (i) species richness and seed bank density are highest in mid-succession habitats, (ii) seed bank variability increases with succession, (iii) the proportion of species in the established vegetation with permanent seed banks decline with succession, (iv) similarity between vegetation and seed bank declines with succession.

**Location:** Mareau-aux-Prés, the Loire River, close to Orléans, France

**Methods:** Seed banks and vegetation were sampled in five habitats from a succession series: (1) Pioneer vegetation of shores and sandbanks, (2) softwood shrubs, (3) softwood forest, (4) mature forest, (5) *Elytrigia*-dominated grasslands. Sample units were 5m x 5m plots. Soil samples were taken from the upper 6 cm. Seed banks were studied via the seedling emergence method, followed by screening of sediment for remaining seeds. Composition of seed banks was compared to that of vegetation using the Sørensen similarity index.

**Results:** Seed bank density varied between 260 and 11260 seeds.m<sup>-2</sup>. Clear differences between habitats existed in the composition of species in seed banks and established vegetation. Seeds of most dominant species were distributed across the whole range of floodplain habitats but were more restricted in the vegetation. Species richness and seed bank densities did not vary with succession as expected, but the proportion of species that produce persistent seed banks did decline with succession.

**Conclusions:** Floodplains of large rivers provide an excellent context to test hypotheses about the processes that influence the links between seed banks and standing vegetation. In the case of high-energy floods and high sediment dynamics, the methods commonly used to study seed banks can however be questioned.

**Key-words:** flooding gradient, floodplain habitats, fluvial islands, Loire LTER, seed bank composition, seed bank density, seedling emergence method, seed extraction, soil seed bank, Sørensen similarity index, seed accumulation index (SAI)

**Taxon nomenclature:** Gargominy et al. 2016

41 **Funding information:** This study is part of the BioMareau project, funded within the framework of the “Plan Loire  
42 Grandeur Nature 2007-2013”. Funding institutions are the “Région Centre Val de Loire” (n°12 DR-RD 27), the European  
43 Union (FEDER programme Présage n°37729), INRA and IRSTEA.

44

45 **1. Introduction**

46  
47 Soil seed banks are a means for plant species to disperse and persist through time, especially in highly variable  
48 environments (Cohen 1966; Venable & Brown 1988). Many authors have investigated the contribution of seed banks  
49 to community assembly (e.g. van der Valk & Davis 1978; Wisheu & Keddy 1991; Boedeltje et al. 2003; Amiaud &  
50 Touzard 2004; Gurnell et al. 2006; Castillo & Stevenson 2010; Araujo Calçada et al. 2015), because they are an  
51 important part of the local species pool. Out of this propagules pool germinants experience a series of environmental  
52 filters which select individuals that are adapted to local conditions (van der Valk & Davis 1978; Keddy 1992;  
53 Hopfensperger 2007). The actual contribution of the soil seed bank to the extant vegetation is the result of several  
54 factors. First, it depends on the extant plant community, because dense, established communities are typically  
55 dominated by C-strategists, i.e. organisms that maximize resource acquisition in productive environments and that  
56 typically develop extensive vegetative structures (Grime 1979). Under such conditions, competition for light or  
57 nutrients is a major environmental filter for community assembly (Amiaud & Touzard 2004; Devlaeminck et al. 2005;  
58 Fraaije et al. 2015b). These conditions contrast with those in early succession stages that offer greater opportunities  
59 for recruitment from the soil seed bank (Fraaije et al. 2015a) or from freshly deposited seeds that may have been  
60 transported by different vectors such as wind, water or animals (Gurnell et al. 2006; Fraaije et al. 2015b). Secondly,  
61 the degree to which seed banks contribute to the assembly of the standing vegetation depends on the composition of  
62 the seed bank in terms of seed longevity and seed dormancy. Ruderal and pioneer species have often been found to  
63 have small, long-living seeds and form a persistent seed bank, i.e. seeds with a viability > 4 years (Thompson et al.  
64 1993; Bekker et al. 1998; Thompson et al. 1998). Many later successional species have larger, short-lived seeds and a  
65 transient seed bank (Decocq et al. 2004; Hölzel & Otte 2004). The generality of these assertions is however open to  
66 question and may depend on local disturbance characteristics (Leishman & Westoby 1998; Hölzel & Otte 2004).

67 When environmental conditions do not allow germination from the soil seed bank, seed bank composition can become  
68 very dissimilar to the floristic composition of standing vegetation. Hopfensperger (2007) reviewed floristic similarity  
69 of seed banks and standing vegetation in wetlands, grasslands and forests. She found similarity to be a function of  
70 ecosystem type, with overall highest similarity values in grasslands, lowest in forests, and intermediate values in  
71 wetlands. The observed ranges of similarity values within each ecosystem type were suspected to depend on dominant  
72 ecosystem processes. In many grasslands, similarity was lowest at early succession stages and increased thereafter,

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73 probably due to limited seed dispersal and seed clustering around the parent plants. In forests, similarity was generally  
74 highest after disturbances and declined thereafter. Wetlands behaved either like grasslands or forests, or showed  
75 unique patterns - presumably linked to vegetation type, hydrological regime or other types of disturbances.

76 Riparian, unconstrained ecosystems are a particularly complex wetland type. They are highly dynamic with regard to  
77 spatial distribution of habitats and plants (Naiman & Décamps 1997). The flow regime in a given floodplain section,  
78 i.e. magnitude, frequency, predictability, flashiness and timing of floods (Poff et al. 1997) determines community  
79 composition and habitat distribution across the floodplain, by sorting plant species according to their flood tolerance,  
80 from more to less flooded sites (Naiman & Décamps 1997; Webb et al. 2012). Habitat dynamics depend largely on  
81 sediment grain size and flow velocity. Water flow has the capacity to move sediment, and acceleration of flow velocity,  
82 e.g. during floods, causes uprooting of plants and remobilization of sediment with grain size below the flow's carrying  
83 capacity. Fluvial wetlands therefore exhibit particularly complex processes of seed dispersal and seed bank formation  
84 in comparison with other ecosystems (Gurnell et al. 2008). In addition to seed rain from existing vegetation,  
85 anemochory and zoochory that drive seed bank formation in terrestrial ecosystems or standing waters, seed dispersal  
86 in perfluvial ecosystems is largely due to hydrochory (Johansson et al. 1996; Leyer 2006; Gurnell et al. 2008; Nilsson  
87 et al. 2010). In low-disturbance ecosystems such as many terrestrial systems, seeds may progressively accumulate  
88 within the substrate, and vertical seed bank structure is therefore commonly used to evaluate the age of the  
89 accumulated seeds (Bekker et al. 1998; Kleyer et al. 2008). This approach may not be appropriate in frequently flood-  
90 disturbed, high-energy floodplains, because deposited sediment and seeds may be remobilized (Gurnell et al. 2008),  
91 i.e. eroded and deposited downstream or elsewhere in the floodplain. The similarity of seed bank composition and  
92 standing vegetation may not be easily predictable under such conditions. Moreover, plant communities from  
93 frequently flooded sites have been shown to have seeds with long floating capacities but rather low seed longevity  
94 (van den Broek et al. 2005), while pioneer habitats in contexts other than frequently flooded riparian ones are  
95 expected to be dominated by species that form permanent seed banks (Thompson et al. 1998). While studies generally  
96 investigate seed banks and extant vegetation on the same scale, Abernethy & Willby (1999) have shown that when  
97 similarity between extant vegetation and seed bank is low, most species missing in the extant vegetation at the plot  
98 scale may be found in the adjacent floodplain. Similarity values are therefore likely to increase when the spatial scale  
99 around sampling plots is increased.

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100 Since Goodson et al. (2001) observed that riparian seed banks are a neglected area of river research, several studies  
101 of riparian seed banks in different geographic contexts have been published (e.g. (O'Donnell et al. 2015; Bourgeois et  
102 al. 2016). Most European studies concentrate on only a small range of habitats: aquatic habitats and backwaters  
103 (Abernethy & Willby 1999; Boedeltje et al. 2004; Combroux & Bornette 2004; Leyer 2006; Fraaije et al. 2015a), pioneer  
104 habitats (Leyer 2006; Corenblit et al. 2016), or floodplain meadows (Hölzel & Otte 2004; Vécirin et al. 2007; Gurnell et  
105 al. 2008). Where river shores are investigated, the studied systems are often low-energy lowland rivers of moderate  
106 size (Boedeltje et al. 2003; Goodson et al. 2003; Gurnell et al. 2006; Gurnell et al. 2008; Araujo Calçada et al. 2015).

107 In this paper we investigate the composition of soil seed banks in relation to standing vegetation in the floodplain of  
108 a large river (*sensu* large river system as defined by Nilsson et al. (2005), i.e. with a virgin mean annual discharge  $\geq 350$   
109  $\text{m}^3 \text{s}^{-1}$ ) with high-energy floods. We investigate the whole range of floodplain habitats, i.e. a wide disturbance gradient.

110 The most frequently and intensely disturbed habitats are regularly flooded and remodelled sand banks with scarce,  
111 mostly herbaceous pioneer vegetation. Their vegetation is typically sparse and dominated by ruderal and river corridor  
112 species. These groups of plants comprise many therophytes whose life cycle is sufficiently short to be completed during  
113 low-water stages (Burkart 2001; Cornier 2002; Greulich et al. 2016). These regularly flooded sites are also where  
114 germination and establishment of pioneer woody species occur. During high-water stages, shores and banks are  
115 typically flooded. In these habitats, persisting woody seedlings (such as *Salicaceae* species) will develop into softwood  
116 shrubs, the second successional stage. They are particularly efficient in slowing down river flow during high-water  
117 stages and thus induce sediment deposits. This process creates an elevation of the alluvial floor that will subsequently  
118 be less frequently flooded. The third successional stage is softwood forest. Hardwood species become established in  
119 its understory, subsequently forming hardwood forest, i.e. the last and only rarely flooded successional stage.

120 We hypothesize that processes involved in seed bank formation greatly differ across the flooding-succession gradient:  
121 vegetation in fluvial pioneer habitats is known to be recruited mainly from flood-dispersed propagules (Leyer 2006;  
122 Fraaije et al. 2015a), while the contribution of seed rain from extant vegetation to the seed bank has been found to  
123 become greater on higher topographic elevations and/or during later successional stages (Gurnell et al. 2006; Fraaije  
124 et al. 2015b), i.e. in less frequently flooded sites (Leyer 2006). Moreover, lower flooding frequency has been shown to  
125 coincide with lower species richness of propagules in the soil seed bank (Andersson et al. 2000). Regarding seed bank  
126 density, one might expect it to be highest in intermediately disturbed sites, i.e. at the intermediate flooding frequency

127 of mid-successional stages. Those sites are still regularly flooded and will thus experience seed import by hydrochory,  
 128 but flow velocity is decreased by existing vegetation, thus giving seed banks a chance to accumulate from both seed  
 129 rain and seed import.

130 Against this background, the present paper aims, first, to describe the composition of seed banks and standing  
 131 vegetation across the habitat gradient in terms of species composition, species richness and seed persistence traits.

132 Secondly, it aims to test the following hypotheses (Fig. 1):

133 H1: Seed bank density, as well as species richness in seed banks and standing vegetation, will be highest  
 134 in mid-succession habitats.

135 H2: Because seed banks in later successional stages are likely to be more influenced by the locally  
 136 established vegetation than by vegetation from the catchment (flood deposits), they will be more  
 137 heterogeneous than seed banks from earlier successional stages.

138 H3: The proportion of species in the standing vegetation that produces permanent seed banks will decline  
 139 with succession and increasing competition (revealed by denser standing vegetation).

140 H4: Similarities between seed bank composition and standing vegetation will decrease along the  
 141 successional gradient, because habitats will be less flood-disturbed, favoring C-strategists with lower seed  
 142 production, lower seed viability and a longer life cycle in standing vegetation.

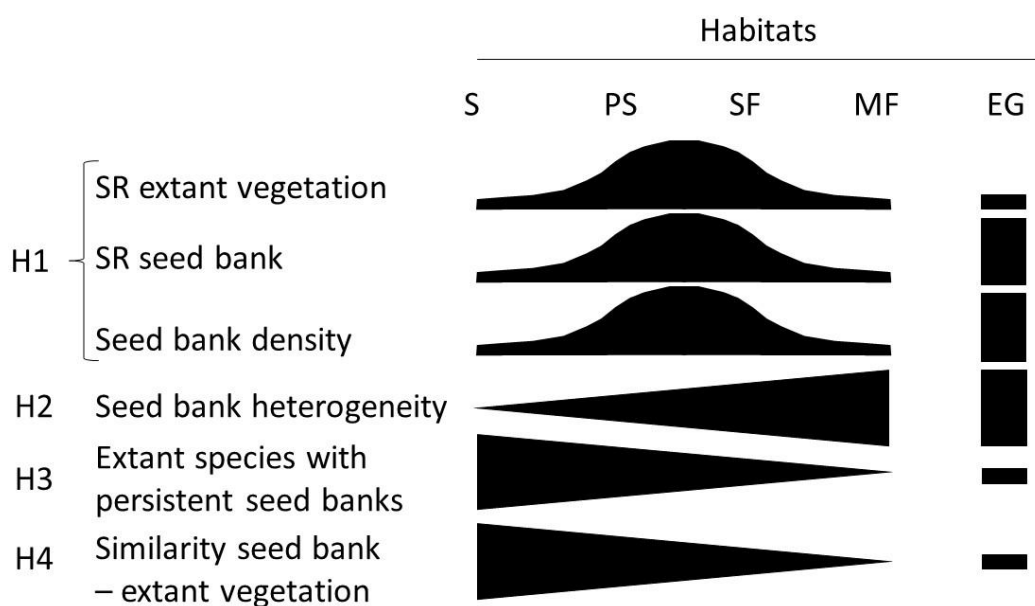


Fig. 1: Summary of hypotheses for the different succession stages (habitats) in the study. The height of the black graph indicates the expected value for each indicator in each habitat. SR: Species richness; S: Sand banks and sandy shores; PS: Softwood (poplar) shrubs; SF: Softwood forest; MF: Mature forest; EG: *Elytrigia*-dominated grassland. For explanations on habitats see section 2.2.

## 2. Methods

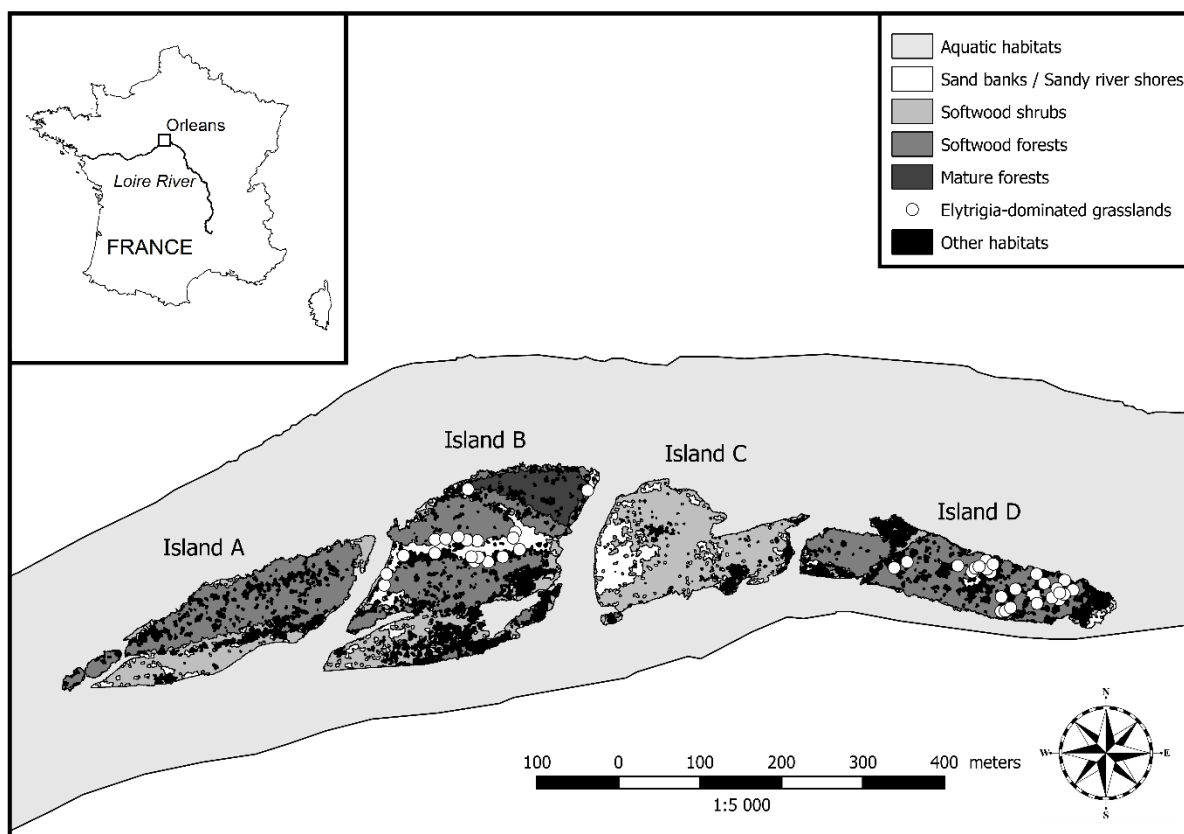
### 2.1 Study site

The study took place at Mareau aux Prés (Loiret, Central France), in the national nature reserve of Saint-Mesmin, about 8 km downstream of the city of Orleans, in the middle reaches of the Loire (47.864413 N, 1.778654 E) (Fig. 2). The Loire is 1020 km in length and is the longest river in France. It rises in the Massif Central in the center of France and flows into the Atlantic Ocean at the city of Nantes. Its catchment area (117 000 km<sup>2</sup>) covers about one fifth of continental France (Oudin et al. 2009). The middle reaches of the Loire extend from the city of Nevers (confluence with the Allier) to the city of Angers (confluence with the Maine). The river here flows freely in a floodplain several hundred meters wide that has been constrained by levees since the Middle Ages (Burnouf et al. 2009). The climate is temperate, with oceanic influences and is relatively mild (643 mm of annual rainfall, 11.3°C average temperature between 1981-2010 in Orleans; Météo France, 2016). The Loire is characterized by an irregular hydrological regime (Cornier 2002) with a coefficient of immoderation > 6, i.e. higher than in other central and western European rivers (Wasson et al. 1993). The average annual discharge of the Loire at the city of Orleans is 340 m<sup>3</sup>.s<sup>-1</sup> (mean interannual discharge years 1964-2017). There is a high amplitude between summer low stages (interannual minimum in August: 97.7 m<sup>3</sup>.s<sup>-1</sup>) and winter flood stages (interannual maximum in February: 596 m<sup>3</sup>.s<sup>-1</sup>) (“Banque Hydro” database, [www.hydro.eaufrance.fr](http://www.hydro.eaufrance.fr)). The low-water stages in summer give rise to numerous sand and gravel banks within the river bed that can be colonized by pioneer plant communities. These habitats are frequently re-modeled by erosion and/or sediment deposition during high-water stages. Plant recruitment mainly occurs when water stages of the Loire decrease in spring (typically April–May). During summer low-water stages, these pioneer habitats are favorable to a range of ruderal species because they offer intense light conditions, a relatively close water table (typically 0 to 1.5 m depending on water stage and topographic elevation) with nutrient-rich river water and little interspecific competition (Greulich et al. 2016). Surficial substrate temperatures may however reach temperatures > 50°C on sunny summer

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172 days (Corillion 1995), and low rooting species may suffer drought stress. Woody pioneer species that are recruited  
173 here include different shrubby *Salix* species (e.g. *Salix purpurea*, *S. triandra*), which are typical for the second  
174 succession stage (shrubby pioneer vegetation), and the softwood tree species *Salix alba* and *Populus nigra*, which will  
175 later form the floodplain's softwood forest (third succession stage). Typical hardwood species on the Middle Loire  
176 River include *Fraxinus excelsior*, *F. angustifolia*, *Ulmus minor*, and *U. laevis*, as well as *Quercus robur* on the least  
177 flooded sites. During winter high-water stages, vegetation on shores and banks, softwood pioneer shrubs together  
178 with softwood forest, are generally flooded. Flooding of transitional and hardwood forests occurs less than yearly. In  
179 addition to these spontaneous succession stages, the floodplain of the Loire also hosts several types of semi-natural  
180 grasslands (Cornier 2002; Boudin et al. 2007); the most frequent are mesophilous to xeric *Elytrigia*-dominated  
181 grasslands. They may be situated at similar topographic levels and thus experience the same flooding frequency as  
182 softwood shrubs or softwood forests.

183 The study site is a 1.5 km-long island complex composed of four islands (Fig 2), situated in a floodplain section (i.e.  
184 area comprised between levees) about 800 m wide. It hosts the whole range of major alluvial habitat types that can  
185 be found in the middle reaches of the Loire: from sparse pioneer vegetation on sandy or gravely river shores and banks  
186 to alluvial transient forest, dominated by *Ulmus minor*.



188 Fig. 2: Location of the study site on the Loire River in France (left) and distribution of major habitats on the studied  
189 Island complex.

## 191 2.2 Vegetation sampling

192 The established vegetation (vascular plants) was sampled in summer 2012 at two different scales: (i) presence of  
193 species throughout the island complex (hereafter called "island scale"), (ii) abundance of species (Braun Blanquet  
194 abundance-dominance index) in 5 m x 5 m plots, hereafter called "plot scale".

195 Sampling on the island scale aimed to be close to exhaustive. Therefore, the island complex was divided into 5 units  
196 (island A, island B north, island B south, island C, island D, Fig. 1) of similar sizes (about 2.5 to 3 ha.) Each unit was  
197 prospected by two experienced botanists for 1 h 45 min, or exceptionally by one botanist for 2 h 40 min, and all the  
198 species they encountered were recorded. If necessary, plant samples were taken for later identification. Sampling for  
199 each unit was repeated three times during the main growing season (mid-July, mid-August and late August) and the  
200 data pooled.

201 Structure and composition of established vegetation at the plot scale was sampled in early August 2012 on the three  
202 most diverse islands (B, C, D). A total of 37 evenly distributed plots were established across the islands in order to  
203 survey the standing vegetation. During the survey, we also sampled the soil seed banks (see below) in 15 plots  
204 encompassing the five most common habitat types (three replicates per habitat type): (i) sand banks or sandy river  
205 shores with scarce pioneer vegetation (S), (ii) softwood (*Populus nigra*) shrubs (PS), (iii) softwood forest (SF), (iv)  
206 mature forest (hardwood-dominated, transitional forest, MF), and also (v) *Elytrigia*-dominated grasslands (EG), a semi-  
207 natural habitat outside the spontaneous succession scheme, situated at topographic positions similar to that of  
208 softwood forests. With regard to the tested hypotheses, *Elytrigia*-dominated grasslands are expected to present a  
209 unique pattern: similar to softwood forests in terms of flooding frequency and seed bank characteristics, and similar  
210 to mature forests with regard to competition among standing vegetation (Fig. 1). For each plot, total percentage plant  
211 cover was visually estimated, as well as Braun-Blanquet abundance-dominance scores for each species.

## 213 2.3 Seed bank sampling and conservation

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214 Soil seed banks were sampled immediately after the assessment of the established vegetation. Nine soil samples per  
215 plot were taken from the upper 6 cm of soil using a 7 cm diameter core sampler. Samples represented a surface area  
216 of 0.0346 m<sup>2</sup> and a volume of 0.0021 m<sup>3</sup> per plot. Soil samples were laid on open trays, covered with tap water and  
217 stored at 4°C over winter. This treatment, which is specific to this study, was presumed to simulate winter conditions  
218 for most vegetation types, since early vegetation stages up to softwood forest are typically flooded during winter, and  
219 flooding of mature forests can occur occasionally. Water was changed every two to three weeks in order to prevent  
220 the formation of biofilms.

### *2.4 Determination of seed bank composition*

223 Seed bank composition was first assessed using the seedling emergence method (Simpson et al. 1998, Combroux &  
224 Bornette 2004). Samples were laid 2 cm thick on 18 cm x 24 cm x 9 cm plexiglass trays on a layer of sand 3.5 cm thick.  
225 The sand had previously been sterilized at 180°C for 6 hours. Samples were divided into two equal parts. One was  
226 submitted to a flooded treatment, presumed to favor germination of aquatic species, the other to a moist treatment  
227 (permanently moist sediment), presumed to favor helophytes and terrestrial plants. Three additional trays with only  
228 sterilized sand were added to each treatment in order to detect contamination. Sample trays were placed randomly  
229 on two tables close to the window, and repositioned randomly once a week. Natural light was complemented between  
230 6 am and 8 pm by fluorescent bulbs with a spectral range adapted to plant growth (Osram Fluora © plant fluorescent  
231 bulb) that were fixed above the trays.

232 All samples were watered once to twice a week with water from the Loire that had previously been filtered through a  
233 40 µm mesh, in order to maintain a constant humidity level. The flooded treatment was oxygenated with aquarium  
234 air bubblers connected to a pump. All samples were kept in the laboratory at room temperature (about 20°C). Trays  
235 were monitored once a week, and seedlings that could be identified were counted and removed. The experiment ran  
236 from April 2013 to April 2014. At the end of the experiment, sediment was examined for remaining seeds. Seeds were  
237 extracted using a protocol based on Grillas et al. (1993). Sediment was sieved at 1 mm, 0.2 mm and 0.125 mm and  
238 coarse material was eliminated. Seeds were separated from sediment by putting each fraction in a recipient with 300  
239 ml of tap water, which allowed floating seeds to be collected. The remaining sediment was visually checked for seeds.

Seeds were dried on filter paper, counted and identified under a dissecting microscope. All seeds found in this study were contained in the 0.2 mm fraction. Identification of seeds was based on Cappers et al. (2012) and personal seed collections. The term “seed bank” in this paper refers to the sum of seedlings and remaining seeds.

## *2.5 Data analysis*

Species richness in seed banks and standing vegetation, as well as seed bank densities, were compared between habitats using Kruskal-Wallis tests after pooling data from the moist and the flooded sub-samples. The results allowed us to test hypothesis H1, i.e. that the highest species richness and seed bank densities would be found in mid-succession stages. Hypothesis H2, i.e. greater heterogeneity in seed bank characteristics in late rather than in early successional stages, was addressed by comparing variances (species richness, densities) across habitat types using the Fligner-Killeen test, which is particularly robust in cases of non-normal distribution of data (Conover et al. 1981). We also examined visually the extent of dispersion among plots from the same habitat on the factorial maps created by multivariate analysis of community composition (see below).

To measure seed persistence traits (hypothesis H3), we calculated Hölzel and Otto’s (2004) seed accumulation index (SAI) for all species found in the seed bank or in the standing vegetation at the plot scale. This index represents the occurrence of species in the seed bank relative to their occurrence in the standing vegetation at the scale of the study site. Seeds that are found solely in the seed bank are presumed to have accumulated through time and therefore to form a permanent seed bank. The index thus overcomes the problem of relatively rare species encountered in field samplings but that do not figure in seed trait databases such as the LEDA (Knevel et al. 2003; Kleyer et al. 2008). We used this index to assess how species that produce accumulating seeds (as a proxy for persistent seed banks) were distributed in the habitat’s standing vegetation.

Similarities between seed bank composition and established vegetation (hypothesis H4) were calculated using the Sørensen similarity index (Sørensen 1948, in Hopfensperger 2007):

$$Q = 2c / (a+b)$$

where a and b are the number of species in the first (seed bank) and second (established vegetation) lists, respectively, and c the number of species occurring in both lists. Similarity was assessed at both plot and island scales.

266 Composition of plant communities (seed bank composition and standing vegetation (plot scale)) was studied in more  
267 detail using multivariate techniques. For each dataset we conducted both a correspondence analysis (CA) on raw data  
268 and a normalized principal component analysis (nPCA). Both ordination techniques analyze data about the floristic  
269 composition of the plots, but they can also be complementary: while PCA highlights the abundant species, CA  
270 highlights rare species (Hill 1973, in Dolédec & Chessel 1991) and focuses on community composition rather than  
271 species abundance (Dolédec & Chessel 1991). These multivariate analyses were followed by between-class analysis  
272 with habitat type as class. We tested for differences in community composition according to habitat using a Monte-  
273 Carlo test with 999 permutations (ade4 package, Thioulouse et al. 1997; Chessel et al. 2004). More detailed studies  
274 were carried out for the 10 most abundant species in the seed bank and extant vegetation. We graphically examined  
275 their distribution across plots, habitats and compartments (i.e. seed bank or standing vegetation), and calculated the  
276 most frequently used index to summarize seed persistence traits, i.e. the seed longevity index according to Bekker et  
277 al. (1998). To do this, we used the records from the LEDA database (Knevel et al. 2003; Kleyer et al. 2008; database  
278 consulted on 28 July 2017). This index is based on information concerning seed longevity type (transient, short-term  
279 persistent, long-term persistent; Thompson et al. 1997). It represents a synthesis (average value) of the seed type  
280 information comprised in available records. Index scores range between 0 (strictly transient) to 1 (strictly persistent).  
281 The index can however only be calculated for species that feature in available databases that reflect knowledge about  
282 the most frequently investigated habitat types. Rare species or species from rarely investigated habitats may be  
283 missing.

284 All analyses were conducted using R version 3.3.2.

### 286 **3. Results**

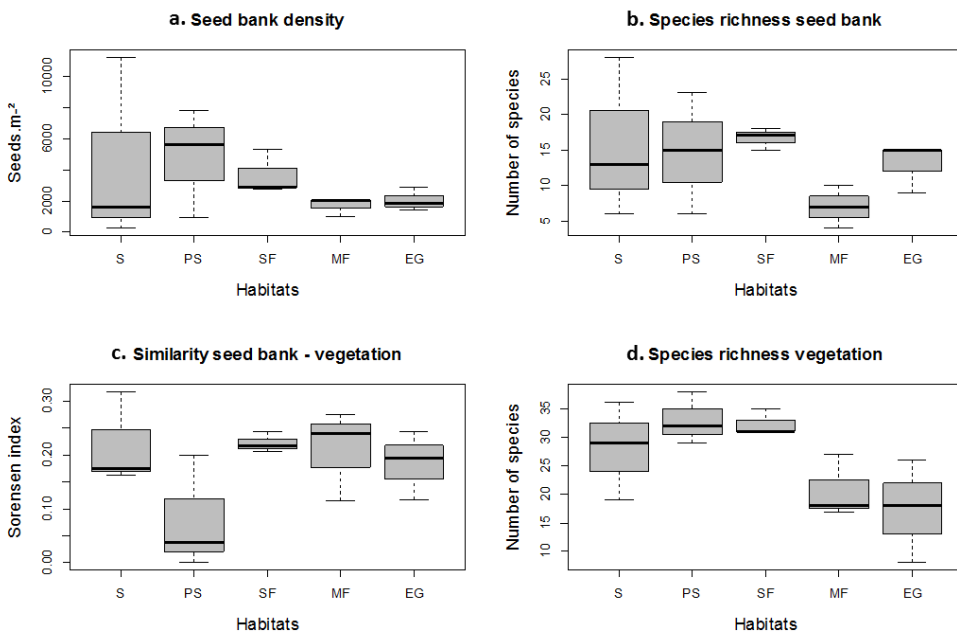
#### 287 *3.1 Seed bank characteristics*

288 The seedling emergence method revealed a total of 816 seeds, 71 resulting from flooded treatment and 745 from  
289 moist treatment. In the remaining sediment, we detected 944 more seeds that had not germinated (482 in the flooded  
290 treatment, 462 in the moist treatment). No germination occurred in the control samples. In all, 35 species were

291 identified. A further 19 species were found after identification of the remaining seeds in the sediment. A total of 84  
 292 seeds could not be identified at species level or remained undetermined.

293 Mean seed density per species at the plot level were  $153 \pm 294$  seeds.m<sup>-2</sup>, with maximum values for *Lindernia dubia*  
 294 (1963 seeds.m<sup>-2</sup>). Species richness at the plot level ranged between 6 and 27 species.

295 Seed bank densities between plots varied between 260 and 11260 seeds.m<sup>-2</sup>. There were no significant differences in  
 296 seed bank density between habitats (Kruskall-Wallis test, p-value=0.678), but variances differed significantly between  
 297 habitats (Fligner-test, p-value < 0.001), with greater variability at the youngest succession stages (S and PS) (Fig.  
 298 3a). Seed banks did also not differ significantly between habitats with regard to median species richness (Kruskal-Wallis  
 299 test, p-value=0.306) (Fig. 3b). Seed banks in mature forest showed a tendency towards the lowest species richness ( $\leq$   
 300 10 species). There were however significant differences between habitats with regard to variability, with greatest  
 301 variance in species richness in sandbanks and under poplar shrubs, i.e. the first two successional stages (Fligner-Killeen  
 302 test p-value 0.01), and lowest variance in softwood and mature forests.



303  
 304 Fig. 3: Characteristics of seed banks and established vegetation across floodplain habitats (plot scale). S: sand banks,  
 305 PS: Softwood (poplar) shrubs, SF: softwood forest, MF: mature forest, EG: *Elytrigia* grasslands.

306  
 307 Species composition of seed banks varied significantly between habitats when CA was applied (between class analysis  
 308 and Monte-Carlo test, 999 permutations, p-value=0.003). The first two axes of the CA explained 45.24% of the

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309 variability contained in the seed bank (Fig. 4a,b). The first axis opposes mainly a small number of forest or widespread  
310 terrestrial species, which were relatively rare in this dataset (positive values), to the more widespread species in the  
311 dataset (center-left of the axis). The second axis is structured mainly by uncommon (in this data set) woodland species  
312 (*Torilis japonica*, *Scrophularia nodosa*, *Poa nemoralis*, *Crataegus monogyna*) that occurred together at one of the  
313 mature forest plots and were associated with negative values on axis 2. Habitats were ordered mainly along the first  
314 axis according to the succession and topographic gradient (S, EG, PS, SF, MF). PCA did not reveal any differences in  
315 seedbank composition (p-value=0.2).

### 317 *3.2 Characteristics of standing vegetation*

318 At the island scale, a total of 293 species were found. The data set from sampling plots comprised 148 taxa (134  
319 species), i.e. 46% of the species from the island scale. As in seed banks, species richness in standing vegetation (plot  
320 scale) presented differences in variance according to habitat (Fligner-Killeen test, p-value = 0.0009). Variability was  
321 greatest in sandbanks and in *Elytrigia* grassland (Fig. 3d). Differences in species richness across habitats were close to  
322 significant (Kruskal-Wallis test, p-value = 0.052). Average species richness in shores, poplar shrubs and softwood forest  
323 was about 30 species, while it was around 20 species in *Elytrigia* grasslands and mature forest.

324 Ordination of plots by PCA explained 26.99% of variation with the first two axes. In CA, the first two axes accounted  
325 for 31.27% of variation. Both techniques separated the different habitats quite clearly (see Fig. 4c for PCA). Species  
326 composition differed significantly between groups with ordination carried out by either PCA or CA (not shown; p-value  
327 = 0.001 in both cases). PCA particularly linked the first axis to a succession gradient with pioneer species and habitats  
328 on the left-hand side and species and habitats from later stages on the right-hand side of the factorial map (Fig. 4d).  
329 While typical shore species and poplar shrub species are both grouped on the upper left-hand side of the factorial  
330 map, species in softwood and mature forest plots appear as a gradient (Fig. 4d).

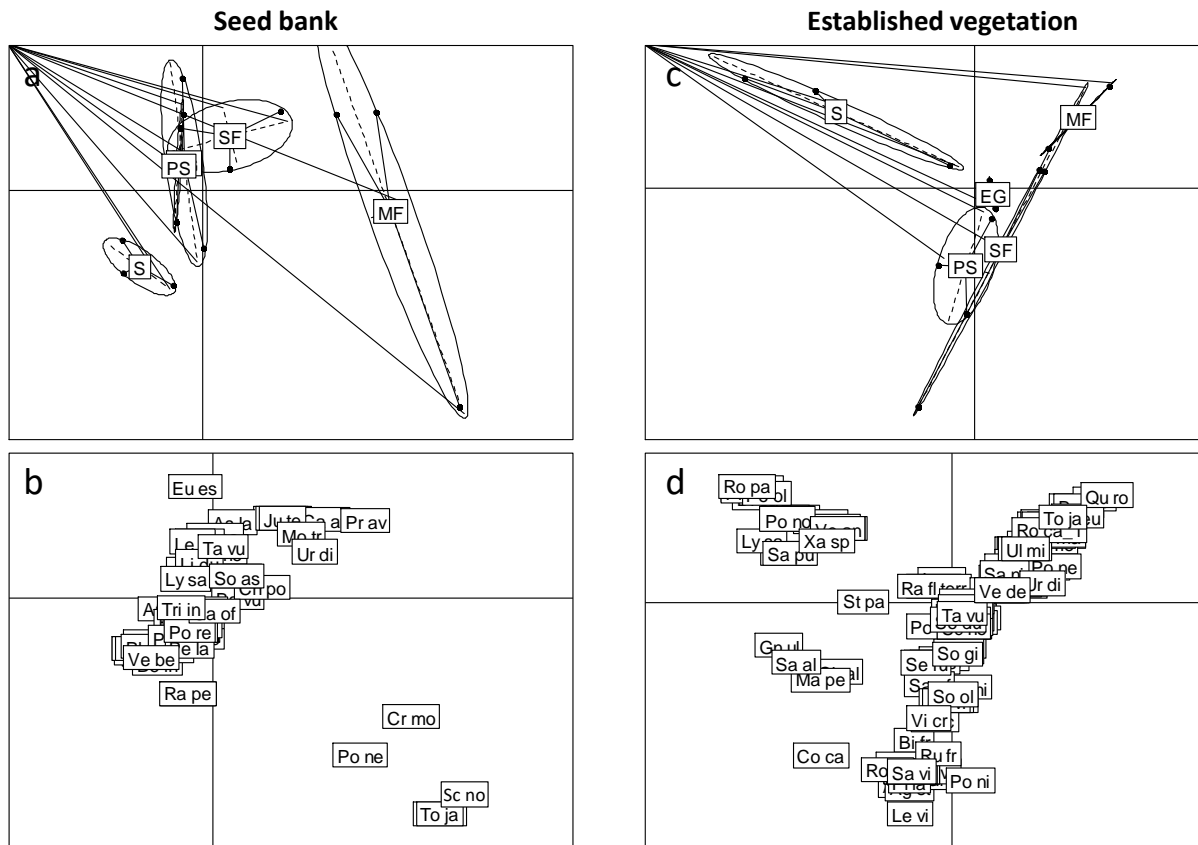


Fig. 4: Ordination of seed bank and standing vegetation according to species composition. Upper plots (a, c): projection of sampling plots (grouped by habitat), lower plots (b, d): projection of species on the factorial maps (axes 1 and 2). Seed bank (left column): ordination by CA; axis 1 accounts for 14.42 % and axis 2 for 12.38 % of total variation. Established vegetation (right column): ordination by normalized PCA; axis 1 accounts for 14.51% and axis 2 for 12.48% of total variation. S: sand banks, PS: softwood (poplar) shrubs, SF: softwood forest, MF: mature forest, EG: *Elytrigia* grasslands. For species labels see Appendix S1.

### 3.3 Comparison of seed banks and standing vegetation

Fifteen taxa were found exclusively in the seed bank (SAI = 100), 95 exclusively in the standing vegetation (SAI = 0), and 40 in both. Among the latter, only 8 taxa were relatively more present in the standing vegetation than in the seed bank (SAI < 50). The proportion of species in the standing vegetation that produce persistent seeds differed according to habitat (Kruskal-Wallis test;  $p=0.0013$ ); SAI-values for the different habitats were: S:  $33.54 \pm 38.62$ , PS:  $14.03 \pm 26.78$ , SF:  $19.67 \pm 29.64$ , MF:  $10.77 \pm 20.93$ , EG:  $17.21 \pm 27.41$ . Median values differed statistically between shores and poplar shrubs ( $p=0.002$ ), and between shores and mature forest ( $p=0.005$ ; Dunn test with Bonferroni adjustment for multiple comparisons).

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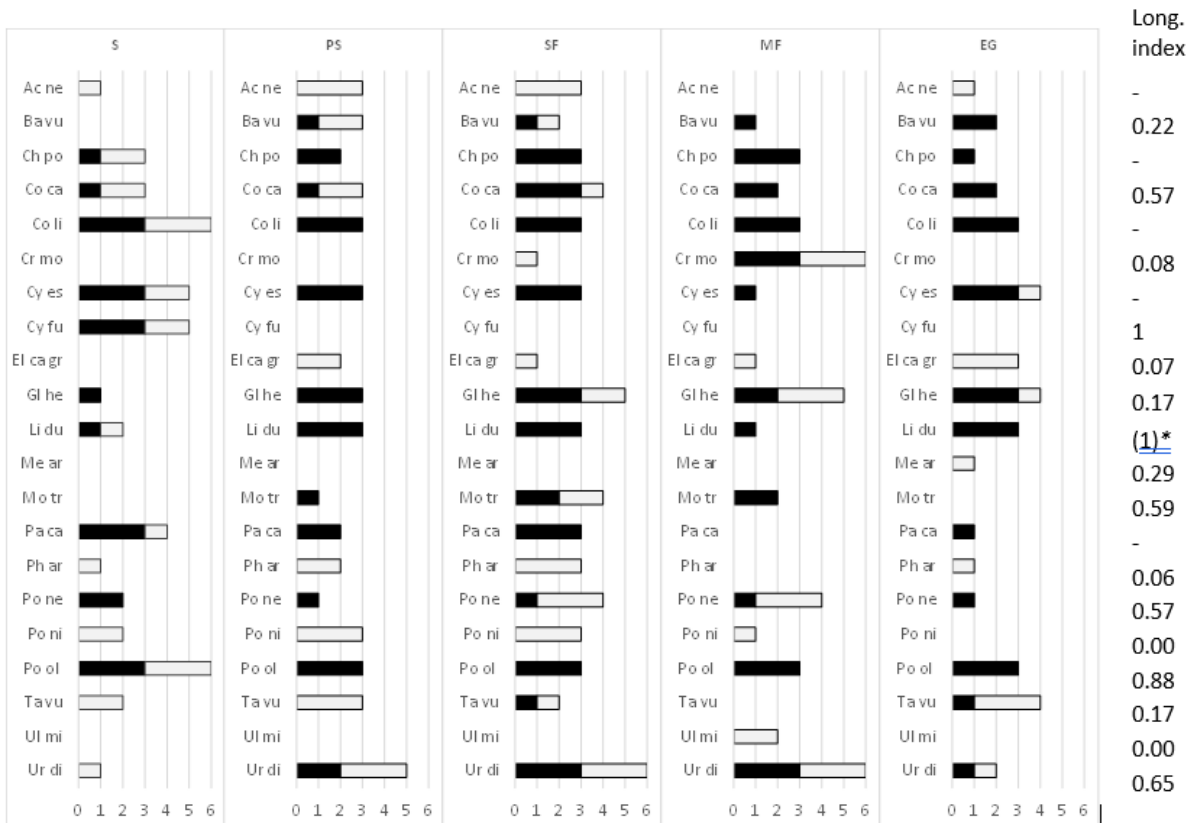
Sørensen similarities between standing vegetation and seed bank ranged between 0 and 0.39 at the plot scale. There were no overall differences between similarity values across habitats (p-value= 0.375, Kruskal-Wallis-test), but there was a tendency for lowest similarities in poplar-shrub habitats (Fig. 3c).

The great majority of species in the seed banks were present in the extant vegetation at the island scale. Exceptions were *Cardamine pratensis* and *Juncus tenageia*, which were found only among seedlings, and *Fragaria moschata*, *Carex demissa*, *Papaver dubium*, *Carex acutiformis*, which were identified only in seeds from sediment. 42 species were common to the seed bank and standing vegetation on the plot scale and 46 species on the island scale. The resulting Sørensen value was 0.35, i.e. similar to the Sørensen values at the plot scale.

#### *3.5 Distribution and traits of the most abundant species*

Both seed banks and standing vegetation were dominated by a small number of species. Three species made up more than 50% of the total numbers of seeds: *Lindernia dubia* (n=412, i.e. 24.6 % of all seeds), *Portulaca oleracea* (n=373, 22.3%) and *Corrigiola litoralis* (n=194, 11.6%). The species that provided more than 50% of total species cover in extant vegetation were *Populus nigra* (28.5% of total cover), *Elytrigia campestris* (11.4%), *Glechoma hederacea* (9.8%) and *Acer negundo* (6.6%). Some species were encountered only in the standing vegetation. This was the case of all woody species with exception of *Crataegus monogyna*, and, among forbs *Phalaris arundinacea*, *Elytrigia campestris* and *Mentha arvensis*. Most species covered however a small range of habitats in the standing vegetation, with a wider range in the seed bank (Fig. 5). Shores were the habitat in which the highest number of species were present simultaneously in the seed bank and in the standing vegetation. Longevity indices based on more than a single record could be calculated for 20 species (Fig. 5). For the majority, available information spanned the whole range of longevity options, i.e. longevity indices were comprised between 0 and 1. Only for *Cyperus fuscus* did all available records (five records) indicate seed bank persistence (short term or long term), and for *Populus nigra* and *Ulmus minor* all available records indicated transient seed banks (eight and three records respectively). For five species, most records indicated persistent seed banks (longevity index > 0.5; based on 11 to 238 records), and for seven species most records indicated transient seed banks (longevity index < 0.5; based on 9 to 270 records).

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372

373 Fig. 5: Seed longevity index and frequency distribution of most abundant species across habitats and compartments.  
 374 Black bars: seed bank; gray bars: standing vegetation. The highest possible frequency score per compartment within  
 375 habitats = 3 (i.e. occurrence in each of the three habitat samples). \* index based on a single record. S: sand banks, PS:  
 376 softwood (poplar) shrubs, SF: softwood forest, MF: mature forest, EG: *Elytrigia* grasslands. For species labels see  
 377 Appendix S1.

378

379 **4. Discussion**

380 The hypotheses tested in this study concerned indicator values (density, species richness, seed accumulation index)  
 381 derived from community composition and plant traits in different habitats. With regard to those indicators, only results  
 382 relevant to hypothesis H3, i.e. the greater presence of species with long-lived seeds in the earliest successional stages,  
 383 corresponds to the expected pattern. There were no significant differences among habitats with regard to species  
 384 richness (seed bank, extant vegetation) and seed bank density (hypothesis H1), and no differences in similarity  
 385 between seed bank and extant vegetation (H4). Concerning hypothesis H2, i.e. the homogenizing effect of flooding on  
 386 seed banks, the reverse pattern to the expected one was observed for species richness of seed banks, i.e. a particularly  
 387 high variability in the earlier successional stages of sand banks and poplar shrubs rather than in floodplain forests.

388

389 *4.1 Findings with regard to H1 and H4*

390 The absence of differences in seed bank densities along flooding gradients (H1 rejected) has been observed by other  
391 authors in the case of rather short gradients with gentle slopes. For example, Haukos & Smith (1994) studied playa  
392 wetlands with topographic less than 1 m, and Bonis et al. (1995) studied shallow Mediterranean wetlands. Clear  
393 differences in seed banks and propagule banks are generally observed across wider gradients such as ours. For  
394 example, James et al. (2007) found highest seed bank densities in habitats with intermediate flooding frequencies in  
395 ephemeral hydrosystems in a semi-arid context, while Abernethy & Willby (1999) detected particularly low densities  
396 of propagule banks in permanently flooded floodplain habitats. Capon & Brock (2006) however found, similar to our  
397 study, differences in taxonomic composition, but no differences seed densities across a wide flooding gradient in  
398 ephemeral desert wetlands. Concerning seed densities, the observed values in our study are situated in the lower  
399 range of what has been observed for other wetland types (see Goodson et al. (2001), Table 1).

400 Compared to seed banks, standing vegetation was more species rich (up to twice more species in the standing  
401 vegetation than in the seed bank at plot scale) and tended to vary more among habitats. Species richness in the  
402 vegetation tended to be lowest in mature forest and *Elytrigia* grasslands, i.e. in the habitat types with the densest  
403 vegetation cover (100% cover for each plot) and presumably the least sediment movement and most stable plant  
404 communities, even if this pattern was not pronounced enough to confirm H1 from a statistical point of view. The  
405 differences in respective species richness of seed banks and standing vegetation (54 and 134 species respectively, data  
406 from all plots pooled) was much more pronounced in our study than in other studies of successional gradients in  
407 riparian ecosystems. Bourgeois et al. (2017) observed slightly more species in the seed bank than in the standing  
408 vegetation (122 and 111 species respectively), while O'Donnell et al. (2015) observed nearly twice as many species in  
409 the seed bank than in the standing vegetation. Similarity values between seed banks and standing vegetation in this  
410 study (mean = 0.15 at the plot scale), were about the lowest range of values found in other studies of riparian systems.  
411 Most studies found that between 20% and 50% of species were common in seed banks and established vegetation  
412 (Gurnell et al. 2006, Beismann et al. 1996, Hughes & Cass 1997, O'Donnell et al. 2015). Vosse et al. (2008) however  
413 found similarity indices varying between 0.1 and 0.56 on four South African rivers, illustrating that a large range of  
414 possibilities exist.

415 Differences in composition between the standing vegetation and the seed bank may be due in part to differences in  
416 seed longevity (Hopfensperger 2007). Within our study, this is obvious when comparing Salicacea to other species  
417 from early succession stages. For example *Populus nigra* is dominant in the vegetation of softwood shrubs and  
418 softwood forest, but absent from the seed bank because of its very short-lived seeds (Stanton & Villar 1996). According  
419 to information found in the LEDA databank (Knevel et al. 2003; Kleyer et al. 2008), most other abundant species have  
420 previously been found to present long-term persistence (see seed longevity indices fig. 5). Exceptions are, besides  
421 *Populus nigra*, *Crataegus monogyna* (short-term persistent) and *Ulmus minor* (short-term persistent). Seed banks in  
422 this study are therefore relatively homogenous in persistence traits, and reasons for differences in similarity values  
423 between standing vegetation and seed banks have to be in factors other than overall short-lived seed banks.

#### 424 425 *4.2 Findings with regard to H2 and H3*

426 The results of this study did not confirm the homogenizing effect of floods for the most exposed habitats (H2 rejected).  
427 Two processes may explain this pattern, as well as the weak similarity between seed banks and extant vegetation in  
428 early succession stages. First, on freshly disturbed spots or newly deposited sediment, high spatial heterogeneity could  
429 be the result of random processes that erode existing seed banks or deposit non-local seeds by hydrochory (Andersson  
430 et al. 2000; Goodson et al. 2003; Gurnell et al. 2008; Moggridge et al. 2009; Araujo Calçada et al. 2015). Secondly, on  
431 previously existing shores in more sheltered zones, high spatial variability may be the result of local seed rain provided  
432 by previously existing plants, i.e. local seed production. Since typical pioneer shore and bank vegetation is sparse, a  
433 patchy seed distribution with high seed densities close to the parent plant could be expected. In a given floodplain  
434 area in highly dynamic systems such as ours, relatively stable zones and highly dynamic zones may be spatially close,  
435 even in pioneer habitats (Rodrigues et al. 2007; Wintenberger et al. 2015). Without further knowledge of previous  
436 sediment dynamics it is therefore not possible to favor one or the other possibility. The methods commonly used to  
437 evaluate a species' seed bank type (transient, short-term persistent, long-term persistent) and that are based on the  
438 depth distribution of the seeds in the soil (Thompson et al. 1997; Kleyer et al. 2008) are clearly not adapted to the  
439 frequently remodeled seed banks in fluvial pioneer habitats. A homogenizing effect of flood deposits may therefore  
440 occur at a greater spatial scale with lower resolution, e.g. on the scale of a river stretch, but not on the plot scale  
441 investigated in this study.

442

443 *4.3 Composition of seed banks and standing vegetation across the floodplain*

444 Despite our findings that similarity values between seed bank and extant vegetation did not differ in this study (H4  
445 rejected), the study revealed clear differences across the floodplain gradient when looking not on indicator values but  
446 on species composition of extant vegetation and seed banks. While differences in standing vegetation across the  
447 floodplain gradient are rather well-known, patterns within seed banks have been less often described. The results of  
448 this study show on the one hand that the most frequent species in the seed banks are present over the full range of  
449 the floodplain gradient, but appear in the standing vegetation in only a small number of habitats. This finding confirms  
450 the existence of seed dispersal across the floodplain over the whole habitat range, by either wind, water or other  
451 vectors. The presence of species from early succession habitats in the seed banks of mature forest was more frequent  
452 than the reverse pattern, indicating a preferential and/or more frequent dispersal from near-channel habitats to the  
453 floodplain. Vegetation from pioneer habitats thus appears to be the greatest contributor to seed dispersion within the  
454 floodplain – a pattern that is consistent with high flooding frequency in early successional stages and seed export and  
455 import by hydrochory. The rather narrow range of species in the standing vegetation can be explained by  
456 environmental filters that differ across floodplain habitats (Keddy 1992; Fraaije et al. 2015b)

457 On the other hand, seed bank composition differed according to habitat. These differences were mainly due to less  
458 frequent species. The results of the multivariate analysis suggest that the most unique seed banks in this dataset were  
459 those of mature forest. This pattern was mainly due to the presence of a small number of typical forest species (*Torilis*  
460 *japonica*, *Poa nemoralis*) that were not present elsewhere. While all other habitats in the study are flooded at least  
461 annually, flooding of mature forest occurs less than yearly, and ecological processes in this habitat may approach those  
462 found in other mature forest types. Late successional forest is one of the most stable ecosystems (Bossuyt & Honnay  
463 2008) in which C-strategists and plant development are favored (Grime 1979), seeds are often large, and seed banks  
464 transient (Thompson et al. 1993; Bekker et al. 1998; Hermy et al. 1999; Bossuyt & Honnay 2008).

465 At the opposite end of the flooding gradient, shores and sand banks are subject to numerous flooding events and  
466 hence to potential seed input within a year. Their most distinctive pattern in this study concerned standing vegetation  
467 rather than seed banks, with the presence of a group of species that were either rare in the dataset (seed banks and

468 extant vegetation) and not found elsewhere (e.g. *Rorippa palustris*) or frequent in the seed banks across the whole  
469 floodplain but only found in the standing vegetation of seed banks and shores (e.g. *Portulaca oleracea*, *Cyperus fuscus*,  
470 *Chenopodium polyspermum*). More distinct patterns in extant vegetation across the floodplain than in the seed bank  
471 have also been observed in hydrologically very different contexts such as desert floodplains (Capon & Brock 2006).

472 The high variability of findings concerning seed banks and their relation to standing vegetation in literature and our  
473 study calls for further studies to disentangle the respective roles of factors likely to influence the relationship between  
474 the composition of standing vegetation and seed banks, such as habitat stability, age and occupation history (Gurnell  
475 et al. 2006), presence of invasive species (Vosse et al. 2008), width of the investigated gradient, as well as intensity  
476 and frequency of flood disturbance. We assume that these contrasting findings depend not only on dominant  
477 ecosystem processes and spatial patterns in standing vegetation and seed banks, but also on differences in sampling  
478 intensity and unit size of sampling plots (sampling efforts on both seed banks and standing vegetation, size of sample  
479 areas, etc).

#### 481 4.4 *Limitations of the study*

482 While this study demonstrated clear differences in composition of seed banks and standing vegetation along the  
483 habitat gradient, the findings with regard to the communities' indicator values did not support most of our hypotheses.  
484 The absence of differences among habitats may, at least partly, be the result of the low numbers of replicate plots per  
485 habitat, particularly given the high variability of early succession stages. Therefore authors wishing to conduct similar  
486 studies can be advised to consider if studying fewer habitats and investing in more plot-scale sampling would be a  
487 better strategy to investigate the questions around which our study is based.

488 In this study, we combined the seedling emergence method with the supplementary, but rarely used step of  
489 quantifying and identifying the seeds that had remained in the sediment. While the first technique may underestimate  
490 actual seed bank densities when experimental conditions cannot meet the whole range of germination requirements  
491 (Gross 1990), the second technique is likely to overestimate the number of viable seeds. The "correct" number of  
492 viable seeds may lie between the two (Corenblit et al. 2016). In this study we presented data from both methods  
493 combined. Most species were either found through the seedling emergence method or in the remaining seeds, but not

in both, suggesting clear differences in ecology and/or detectability. This point, together with methodological considerations of seed bank studies in the floodplain of large, dynamic rivers will be developed elsewhere (Greulich et al. in prep.).

**Acknowledgements:** We wish to thank Yann Fillatre and Cécile Gaudet for field work and seed identification, Hilaire Martin and Anne Vellemeijer for field work assistance, and Karl Matthias Wantzen and Joe Greet for helpful comments on the manuscript. Thanks go also to Michel Chantereau and Damien Hémeray from the national nature reserve of Saint-Mesmin for their interest and their support for science at the Mareau Islands, to Fabien Verniest for his contribution to cartography and to Elizabeth Yates for linguistic assistance. The comments of two anonymous referees greatly improved the manuscript.

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