



**HAL**  
open science

# Can vegetation clearing operations and reprofiling of bars be considered as an ecological restoration measure? Lessons from a 10-year vegetation monitoring program (Loire River, France)

Philippe Janssen, Richard Chevalier, Michel Chantereau, Rémi Dupré, André Evette, Damien Hémeray, Anders Mårell, Hilaire Martin, Stéphane Rodrigues, Marc Villar, et al.

## ► To cite this version:

Philippe Janssen, Richard Chevalier, Michel Chantereau, Rémi Dupré, André Evette, et al.. Can vegetation clearing operations and reprofiling of bars be considered as an ecological restoration measure? Lessons from a 10-year vegetation monitoring program (Loire River, France). *Restoration Ecology*, 2023, 31 (3), pp.1-31. 10.1111/rec.13704 . hal-03713671

**HAL Id: hal-03713671**

**<https://hal.inrae.fr/hal-03713671>**

Submitted on 30 Jun 2023

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 **Can vegetation clearing operations and reprofiling of bars be considered as an ecological restoration**  
2 **measure? Lessons from a 10-year vegetation monitoring program (Loire River, France)**

3

4 **RUNNING HEAD:** Fluvial maintenance works restore riparian habitats

5

6 Philippe Janssen<sup>1\*</sup>, Richard Chevalier<sup>2</sup>, Michel Chantereau<sup>2</sup>, Rémi Dupré<sup>3</sup>, André Evette<sup>1</sup>, Damien Hémeray<sup>2</sup>,  
7 Anders Mårell<sup>4</sup>, Hilaire Martin<sup>4</sup>, Stéphane Rodrigues<sup>5</sup>, Marc Villar<sup>6</sup>, Sabine Greulich<sup>5</sup>

8

9 <sup>1</sup> Univ. Grenoble Alpes, INRAE, LESSEM, F-38402 St-Martin-d'Hères, France

10 <sup>2</sup> Loiret Nature Environnement, F-45100 Orléans, France

11 <sup>3</sup> Conservatoire Botanique National du Bassin Parisien, F-45064 Orléans, France

12 <sup>4</sup> INRAE, EFNO, F-45290 Nogent-sur-Vernisson, France

13 <sup>5</sup> UMR CNRS 7324 CITERES, Univ. De Tours, F-37200 Tours, France

14 <sup>6</sup> INRAE, ONF, BioForA, F-45075 Orléans, France

15

16 ORCID

17 Philippe Janssen: 0000-0003-3310-0078

18 André Evette: 0000-0002-0927-0037

19 Anders Mårell: 0000-0002-3328-4834

20 Stéphane Rodrigues : 0000-0002-5519-125X

21 Marc Villar: 0000-0001-9210-7072

22 Sabine Greulich: 0000-0001-5678-6944

23

24 \* Corresponding author, email [philippe.janssen@inrae.fr](mailto:philippe.janssen@inrae.fr), phone +33 476762879

25

26 **Author contributions:** RC, SR, MV conceived and designed the research; RC, MC, RD, DH, HM collected the  
27 data; PJ analyzed the data; PJ wrote the first draft of the manuscript; RC, AE, AM, SR, MV, SG edited the  
28 manuscript.

29 **ABSTRACT**

30 Maintenance operations in regulated rivers are often implemented as preventive measure to maintain wide,  
31 smooth channels and to limit the risk of flooding. By clearing vegetation, removing roots and lowering  
32 sediment bar elevation, these works can recreate pioneer habitats and related plant communities. Using a  
33 before-after-control-impact design with monitoring of riparian vegetation over 10 years, we evaluated the  
34 effects of fluvial maintenance works on plant richness and composition in an island complex located in a Nature  
35 Reserve along the Middle Loire River. Our results showed that artificial rejuvenation operations had a  
36 significant short-term negative effect on richness. However, in the few years following the work, the riparian  
37 communities established on the rejuvenated island became more diverse, with a large proportion of annual  
38 plants, contributing to the increased species pool of the Nature Reserve. In addition, we found that temporal  
39 changes in species richness were strongly influenced by hydrological conditions, with a peak in biodiversity  
40 observed during prolonged summer low water. This highlights the importance of considering flow variations to  
41 more accurately assess the ecological benefit of restoration operations on riparian vegetation. Overall, as  
42 successional stages were more advanced at the island complex scale, fluvial maintenance works have allowed  
43 the recreation of sandy pioneer habitats exposed to flooding. These habitats have promoted the establishment  
44 of species-rich communities without favoring the installation of invasive alien species. From this view, the  
45 maintenance works have increased the mosaic of habitats within the Nature Reserve and have restored  
46 environmental conditions favorable to early-successional species.

47

48 **KEYWORDS:** biodiversity, conservation, floods risk management, pioneer habitats, rejuvenation, riparian  
49 plants, sandbar

50

51 **IMPLICATIONS FOR PRACTICE:**

- 52 - Clearing operations, if accompanied by a lowering of the topographic level of alluvial bars, can benefit  
53 pioneer riparian plant communities and thus be viewed as a means of assisting in the restoration of  
54 regulated rivers with vegetation encroachment
- 55 - The lowering of the topographic level must be done in such a way as to promote a greater frequency  
56 of flooding, allowing the establishment of pioneer annual species and native tree seedlings

- 57 - Monitoring programs for these operations require a long-term investment and must take into account  
58 seasonal and interannual flow variations
- 59 - When the dynamics of disturbances are still active, the principle of non-intervention should be favored  
60 to diversify the mosaic of riparian habitats in the riverbed

61

## 62 **INTRODUCTION**

63 In river ecosystems, strong interactions between water-sediment flows and vegetation shape geomorphic  
64 surfaces (Corenblit et al. 2009; Gurnell et al. 2012). By trapping, accumulating and stabilizing sediments of  
65 different sizes (Wilkes et al. 2019) and responding to associated geomorphic changes (Corenblit et al. 2015),  
66 aquatic and riparian vegetation enable the construction of a mosaic of complex riverbed habitats (Junk et al.  
67 1989) that benefit a large number of species (Ward et al. 1999; Dudgeon et al. 2006). Conversely, high water  
68 flows are capable of remobilizing fine and coarse sediments, but also of uprooting or burying plant species,  
69 thus causing riparian habitat renewal (Polzin & Rood 2006; Wintenberger et al. 2019). Flood-related  
70 disturbances are therefore a key element in the dynamics of riparian habitats - bars, islands, banks - and, more  
71 generally, in the functioning of river ecosystems (Naiman & Decamps 1997).

72 Due to large variations in their frequency, intensity, duration and timing, flood disturbances are difficult to  
73 predict in space and time (Poff et al. 1997). For rivers subject to a pluvio-nival regime, lower water levels during  
74 the summer period allow specialized pioneer plant communities to colonize and establish on exposed sand or  
75 gravel surfaces (Gurnell et al. 2001; Kalníková et al. 2018). If these surfaces are not too heavily reshaped by  
76 erosion and/or sediment deposition during winter and spring high water phases, vegetation establishment can  
77 continue and succession can be initiated (Corenblit et al. 2015; Caponi et al. 2019). Thus, in just a few decades,  
78 local abiotic conditions, i.e., the accumulation of fine sediments and relative surface elevation, and biotic  
79 conditions, i.e., species composition and biomass accumulation, can change markedly (Egger et al. 2015;  
80 Muñoz-Mas et al. 2017; Janssen et al. 2020). In the absence of high-magnitude floods, e.g., due to the presence  
81 of flood retention dams upstream, the process of terrestrialization, i.e., the process by which former aquatic  
82 areas evolve towards a terrestrial ecosystem as a result of dewatering and/or sedimentation, may be initiated  
83 (Tracy-Smith et al. 2012). Coupled with the gradual encroachment of vegetation on these newly emerged  
84 surfaces, a greater uniformity of environmental conditions at the river reach scale can be expected (Ward &  
85 Stanford 1995). This may hinder the maintenance of riparian species of conservation concern that require

86 specific habitat conditions, such as a highly disturbed environment for pioneer annual plant species (e.g.,  
87 Rottenborn et al. 2018) or sandbars for bird nesting (e.g., Catlin et al. 2015). Overall, these processes may  
88 result in an increase in taxonomic and functional similarities of riparian communities over time (i.e., biotic  
89 homogenization, Olden & Rooney 2006).

90 Beyond the potential ecological consequences, vegetation encroachment is also seen as an important  
91 adjustment process that river managers aim to control in order to maintain wide, smooth channels and limit  
92 the risk of flooding for nearby human settlements and activities (Vargas-Luna et al. 2015). Therefore, even in  
93 unregulated rivers, riverbed maintenance works are often conducted by clearing vegetation, removing root  
94 systems and lowering the topographic levels of alluvial bars. Despite their primary hydraulic objectives,  
95 maintenance works can also promote sediment remobilization and thus compensate for a hydrosedimentary  
96 regime altered by human activities (dams, bank protection, groynes, sediment mining...). In this view, it can be  
97 expected that these works will result in the recreation of young patches of pioneer vegetation (Geerling et al.  
98 2008) that will stimulate plant succession and thus increase the ecological value of riparian zones. Conversely,  
99 rejuvenation operations, by offering new alluvial surfaces that can be quickly colonized by annual riparian  
100 communities, can also promote colonization by undesirable invasive alien species (Planty-Tabacchi et al. 1996;  
101 Richardson et al. 2007). Vegetation maintenance works in riverbeds, if they increase the mosaic of riparian  
102 habitats and favor the development of native, pioneer communities could therefore be considered as a form of  
103 ecological restoration, i.e., a way to assist the recovery of an ecosystem that has been degraded, damaged, or  
104 destroyed (Gann et al. 2019).

105 We aimed to study the response of riparian vegetation to clearing operations and reprofiling of bars in a sandy-  
106 gravel bed river with active floodplain dynamics. By taking a comparative approach before and after fluvial  
107 maintenance works on a pioneer island in the main channel, by comparing vegetation dynamics with  
108 unmanaged islands located downstream and upstream (i.e., before-after-control-impact design), and by  
109 following successional trajectories of the three islands over 10 years, we seek to assess the added ecological  
110 value of the clearing works. Although numerous studies have documented the response of riparian vegetation  
111 to various hydro-geomorphic restoration strategies, most field campaigns using successive vegetation surveys  
112 after restoration have been conducted over a short period of time, i.e., less than 6 years (González et al. 2015).  
113 However, obtaining information on the response of riparian vegetation over a longer time scale appears  
114 fundamental to assess the adequacy of these maintenance works for restoring the ecological integrity of

115 riparian communities. This should help to develop more effective management strategies for riparian  
116 environments by allowing the expression of a mosaic of diversified habitats. Also, beyond the direct effect of  
117 maintenance works, several environmental parameters, such as interannual changes in hydrological and  
118 climatic conditions in the year and/or growing season before vegetation development, can have a strong  
119 influence on the dynamics of riparian habitats (e.g., Vervuren et al. 2003; van Eck et al. 2004; Kalníková et al.  
120 2018). Disentangling the effects of maintenance works from those related to changes in environmental  
121 conditions on the diversity and composition of riparian plant communities is therefore fundamental to better  
122 understand the ecological added-value of restoration operations.

123 Within this framework, and more precisely within the research program “BioMareau”, aiming at understanding  
124 the effect of maintenance works on bar morphodynamics, seed banks and vegetation dynamics of an island  
125 complex located in the National Nature Reserve of Saint-Mesmin along the Middle Loire (Wintenberger et al.  
126 2015, 2019; Greulich et al. 2019), we addressed the following two questions: (i) What are the effects of  
127 maintenance works on riparian plant species richness and composition? (ii) Are these variations in riparian  
128 species richness and composition related to interannual changes in hydrological or climatic conditions?  
129 Because an increase in biodiversity by itself cannot be considered a restoration success, for each of these two  
130 questions we also studied the individual response of species and species groups, i.e., species with an annual life  
131 cycle, species of conservation concern, and invasive alien species, at the scale of the island complex and at each  
132 individual island. This was done to evaluate more precisely the ecological benefits of the maintenance works  
133 conducted on the riparian habitats of the Nature Reserve, but also to better understand the evolution of  
134 biodiversity on the three islands in relation to the variations of environmental parameters on the Loire River.

135

## 136 **METHODS**

### 137 **Study area and experimental design**

138 The study was conducted along the Loire River (total length = 1,006 km, catchment area = 117,356 km<sup>2</sup>) in its  
139 middle reach (mean annual discharge = 365 m<sup>3</sup>/s, Figure 1). This large river (Strahler number at the mouth of 8)  
140 is regulated by several dams in the upstream part of its watershed, including those of Villerest and Grangent,  
141 located respectively at 330 km and 410 km upstream from Orléans, which can reduce flood peaks and release  
142 water during low flow periods. The islands complex is composed of four islands all located within the perimeter  
143 of the National Nature Reserve of Saint-Mesmin, about 10 km downstream of Orléans (central France). This

144 reserve extends along a 9 km stretch of the Loire River and covers an area of 263 ha included in the inter-dike  
145 space separating the active channel from the floodplain. It protects mainly water surfaces of the main and  
146 secondary channels, as well as bars composed of sand and gravel, more or less colonized by riparian  
147 vegetation. This area is characterized by a temperate climate with oceanic influences (mean annual  
148 temperatures of 11.3°C and annual precipitation of 643 mm). On this section, the Loire River flows freely in a  
149 several hundred meters wide floodplain that has been constrained by levees since the Middle Ages (Burnouf et  
150 al. 2009). The hydrological regime is characterized by a large amplitude in water levels. Summer low stages  
151 allow the emergence of numerous sandy gravel bars in the riverbed, and winter/spring flood stages can  
152 reshape the fluvial landforms through erosion/accretion processes.

153 Over ten summers between 2012 and 2021, we sampled three islands, each with a comparable area of 2.5 to 3  
154 ha, belonging to a 1.5 km-long island complex located in the downstream part of the Nature Reserve (Figure 1).  
155 The fourth island was not taken into account in the analyses because its surface is too large, i.e., 4.8 ha,  
156 compared to the three studied islands, which could bias the results based on comparisons. This island complex  
157 consists of non-migrating islands in the mid channel conditioned by three geometrical forcings: the presence of  
158 a riffle, the curvature of the channel, and the widening of the riverbed (Wintenberger et al. 2015). These  
159 islands show a typical sediment grainsize fining upwards from pebbles to sands. They host the full range of  
160 major alluvial habitat types found in the Loire middle reach, i.e., from sparse pioneer vegetation on sandy or  
161 gravely bars to alluvial forests dominated by post-pioneer species. As part of the flood risk management plan,  
162 the Departmental Directorate of Territories of the Loiret cleared the vegetation, including roots, and lowered  
163 the topographic level of the central island in September 2012, hereafter referred to as the “rejuvenated  
164 island”, to maintain flow capacity during floods and avoid the reduction of its active width (elevation of the  
165 channel bottom = 82.5 m, rejuvenated island = 84.9 m, downstream island = 85.3 m, upstream island = 86.5 m).  
166 As a result of the rejuvenation operations, this island was transformed into an homogeneous bare and flat  
167 sandy gravel bar of 2.67 ha on which bedload sediment mobility occurred during the floods that occurred after  
168 the maintenance works (Wintenberger et al. 2015). In 2013, the typical longitudinal grain size fining  
169 characterizing alluvial bars was observed identifying two areas of the rejuvenated island: the upstream one  
170 (stable area) was made of coarse sediments like pebbles and sediment mobility was reduced; the downstream  
171 one (mobile area) was mainly made of sands and gravels, characterized by high sediment mobility during floods  
172 and significant mortality of woody vegetation seedlings (Wintenberger et al., 2019). Although having different

173 management histories, the vegetation in the downstream (i.e., colonized by trees in the 1990s and never  
174 managed since) and upstream (i.e., colonized by trees before the 1970s and clear-cut in 1995) islands was not  
175 affected by the maintenance work performed in 2012. These two islands are therefore used here as control  
176 areas to compare with the rejuvenated island.

#### 177 **Vegetation data**

178 At the scale of each island (i.e., sampling unit,  $n = 3$ ), the vegetation was surveyed using a method known as  
179 whole-plot floristic inventories (Chevalier et al. 2010). This method is suited to inventorying a large number of  
180 species, including the rarest (see e.g., Tabacchi et al. 1996). This close to exhaustive method consists in  
181 surveying sampling units of similar size, herein islands of about 2.5–3 ha each, during a controlled research  
182 time of 1.75 hours for 2 persons or 2.67 hours for one person (excluding the time of determinations using  
183 identification keys), where all the vascular plants at least partly rooted in terrestrial conditions are noted (i.e.,  
184 excluding partially submerged macrophyte species). To characterize the entire plant community, account for  
185 plant phenology and insure the reproducibility of the observations, three complete surveys were conducted  
186 per year (late June, late July and early September) on each island trying to cover the whole area of the sampling  
187 unit at each pass. To limit observer biases, all surveys were performed by the same experienced botanist team.  
188 The list of inventoried species was cross-referenced with several local, regional and national lists of plant  
189 species in order to single out three sub-groups of species (Table S1). The group “annual” includes species that  
190 complete their life cycle in less than a year, i.e., therophytes based on plant life-forms (Raunkiaer 1934). The  
191 presence of these species often characterizes the pioneer state of riparian habitats. The group “heritage”  
192 includes species with the highest conservation value, i.e., protected species, regionally threatened or near-  
193 threatened species, species characteristic of zones with high ecological value at the regional scale and very rare  
194 indigenous species along the studied Loire reach (Cordier & Filoche 2016). The maintenance of these heritage  
195 species in a good state of conservation represents a priority issue for the managers of the Nature Reserve. The  
196 group “undesirable” includes species belonging to the hierarchical lists of invasive alien species in the region  
197 (Desmoulins & Emeriau 2017) or in the Loire watershed (Méheust & Varray 2020) as well as exogenous species  
198 escaped from gardens or crops in the region (Cordier & Filoche 2016). The presence of these undesirable  
199 species in the Nature Reserve represents a potential threat to native species and challenges conservation and  
200 restoration measures.

#### 201 **Hydrological and climatic attributes**



202 To take into account the variations of the hydrological and climatic conditions across the 10 years of vegetation  
203 monitoring, we extracted data from two different sources. For the hydrological attributes, we extracted  
204 discharge data of the Loire River at the nearest gauging station, i.e., the Pont Royal station, 10 km upstream of  
205 the studied island complex in the city center of Orléans (data available at : <http://www.hydro.eaufrance.fr>).  
206 Between Orléans and the studied islands, only a small tributary from a resurgence of the Loire influences the  
207 hydrology (Loiret, total length = 11 km, catchment area = 252 km<sup>2</sup>, mean annual discharge = 1 m<sup>3</sup>/s). This  
208 gauging station delivers discharge data with several measurements per day. From these data, we calculated the  
209 mean and the maximum discharge at two time-scales: during the year prior to vegetation sampling, i.e., from  
210 September 1 to August 31, and during the vegetation-growing season, i.e., from May 1 to August 31 (Table S2).  
211 For the climatic attributes, we extracted air temperature and precipitation data from the weather station  
212 Orléans-Bircy about 15 km north of the island complex. From these data, we calculated the mean air  
213 temperature and total precipitation at two time-scales: during the year prior to vegetation sampling, i.e., from  
214 September 1 to August 31, and during the vegetation-growing season, i.e., from May 1 to August 31 (Table S2).

215 **Statistical analysis**

216 To study whether total, annual, heritage and undesirable species richness varied over time, before and after  
217 maintenance works, we used species accumulation curves at two spatial scales. At the scale of the island  
218 complex, we considered all the species recorded on the three islands during at least one of the three botanical  
219 surveys conducted each year (n = 9). At the scale of each island, we considered all the species inventoried  
220 during at least one of the three botanical surveys conducted each year (n = 3), this for the downstream island  
221 (i.e., used as a control), the rejuvenated island and the upstream island (i.e., used as a control). Then, to  
222 determine whether cumulative species richness at both scales differed between the baseline year (2012, i.e.,  
223 pre-impact) and each of the 9 years following fluvial maintenance works (2013-2021, i.e., post-impact), we  
224 used Monte Carlo randomization tests (n = 999) (rich package, Rossi 2011).

225 To determine whether interannual variations in cumulative species richness at both scales were related to  
226 variations in hydrological and climatic conditions between years, we used the Spearman's rank correlation  
227 coefficient and tested for the significance of the relationship by rank order between both sets of variables after  
228 adjusting the p-value with the Benjamini and Hochberg correction.

229 To determine whether species composition varied between islands and years, we used PERMANOVAs with 999  
230 permutations (vegan package, Oksanen et al. 2013). We also performed pairwise comparisons between the

231 three islands and between the baseline year 2012 and each of the 9 years following fluvial maintenance works  
232 (p-value adjusted with the Benjamini and Hochberg correction). These analyses were based on a Sørensen-Dice  
233 distance matrix using the presence-absence of each plant species present in at least 10 % of the vegetation  
234 surveys. Since dissimilarity may be related to differences in species richness, we quantified the nestedness  
235 pattern in a presence/absence matrix using the NODF metric (Almeida-Neto et al. 2008) and compared  
236 observed patterns with those resulting from a fixed-fixed null model, i.e., where the sums of the rows and  
237 columns are fixed, with 999 permutations (Ulrich et al. 2009).

238 To determine the ecological associations of individual species with the three islands and the 9 years following  
239 fluvial maintenance operations, we used the phi coefficient of association, i.e., a measure of association  
240 between two binary variables (indicspecies package, De Cáceres & Legendre 2009). Because species  
241 composition changes on the rejuvenated island between 2012 and 2013 were mainly caused by maintenance  
242 works, pre-work vegetation surveys were discarded (i.e., 2012, n = 9). Then, we used the phi index to  
243 investigate plant species associations with the downstream island, the rejuvenated island or the upstream  
244 island and with each of the years between 2013 and 2021 and tested the statistical significance of the  
245 associations using permutation tests (n=999).

246 To determine whether interannual variations in hydrological and climatic conditions between years explained  
247 differences in plant composition, we used canonical analysis of principal coordinates (CAP, Anderson & Willis  
248 2003), based on the same Sørensen-Dice distance matrix as previously, with 999 permutations (vegan package,  
249 Oksanen et al. 2013). As we knew that differences in species richness were driving variations in plant  
250 composition, we added the richness as a condition in the CAP in order to remove its effect from the analysis.  
251 Then, we calculated the marginal contribution of the mean and maximum discharge and of the mean  
252 temperature and total precipitation during the vegetation-growing season and tested for their individual  
253 significance (after all other variables were partialled out). To illustrate species response to environmental  
254 parameters, we also extracted species scores along the first two axes of the CAP.

255 Analyses were performed with R version 3.5.1 (R Core Team 2020).

256

## 257 **RESULTS**

258 In total, 422 plant species were recorded on the three studied islands during the 10 years of vegetation  
259 monitoring. Among these, 156 species were annual, 47 species were considered as heritage species (one

260 species was protected at national level and two species at regional level) and 44 species as undesirable species  
261 (31 species were listed as invasive alien species) within the riparian habitats of the Loire River (Table S1).  
262 Specifically, 319 plant species were inventoried on the downstream island, 329 species on the upstream island  
263 and 277 species on the rejuvenated island.

#### 264 **Changes in cumulative species richness from the 2012 baseline year**

265 At the island complex scale and as compared to the baseline year 2012 (Figure 2 & Table S3), the total  
266 cumulative species richness was significantly lower in 2013 ( $p = 0.001$ ) but significantly higher in 2017 ( $p =$   
267  $0.003$ ) and 2019 ( $p = 0.001$ ). The cumulative richness of annual species was significantly lower in 2013 ( $p =$   
268  $0.001$ ) but significantly higher in 2014 ( $p = 0.008$ ), 2017 ( $p = 0.001$ ) and 2019 ( $p = 0.001$ ). The cumulative  
269 richness of undesirable species was significantly higher in 2014 ( $p = 0.010$ ), 2015 ( $p = 0.029$ ), 2016 ( $p = 0.023$ ),  
270 2017 ( $p = 0.005$ ), 2019 ( $p = 0.028$ ) and 2021 ( $0.006$ ).

271 At the individual island scale (Figure 3 & Table S3), as compared to the baseline year 2012, the total cumulative  
272 species richness was significantly lower in 2013 ( $p = 0.041$ ), the cumulative richness of annual species was  
273 significantly lower in 2013 ( $p = 0.045$ ) but was significantly higher in 2019 ( $p = 0.042$ ) and the cumulative  
274 richness of heritage species was significantly lower in 2013 ( $p = 0.040$ ) and 2014 ( $p = 0.046$ ) on the rejuvenated  
275 island. In addition, the cumulative richness of annual species was significantly lower in 2013 ( $p = 0.048$ ) but was  
276 significantly higher in 2019 ( $p = 0.041$ ) on the downstream islands. None of the cumulative species richness  
277 parameters varied significantly between the baseline year and the 9 years of vegetation monitoring on the  
278 upstream island.

#### 279 **Influence of interannual variations in hydrological and climatic conditions on cumulative species richness**

280 At the island complex scale, Spearman's rank order correlation test revealed that cumulative species richness  
281 decreased significantly with increasing mean (total,  $p = 0.025$ ; annual,  $p = 0.025$ ) and maximum (total,  $p =$   
282  $0.032$ ; heritage,  $p = 0.025$ ) discharge during the year prior to vegetation sampling as well as with increasing  
283 mean (total,  $p = 0.015$ ; annual,  $p = 0.025$ ) and maximum (total,  $p = 0.015$ ; annual,  $p = 0.001$ ) discharge during  
284 the vegetation-growing season (Table S4). No significant correlation existed with regard to climatic conditions.  
285 In contrast, the cumulative richness of undesirable species was not affected by interannual variations in  
286 hydrological and climatic conditions.

287 At the individual island scale, Spearman's rank order correlation test confirmed the importance of hydrological  
288 conditions on richness patterns. For the downstream island, the cumulative species richness decreased

289 significantly with increasing maximum (total,  $p = 0.032$ ; annual,  $p = 0.038$ ) discharge during the year prior to  
290 vegetation sampling as well as with increasing mean (total,  $p = 0.029$ ; annual,  $p = 0.003$ ) and maximum (annual,  
291  $p = 0.008$ ) discharge during the vegetation-growing season (Table S4). For the rejuvenated island, the  
292 cumulative species richness decreased significantly with increasing mean (total,  $p = 0.024$ ; annual,  $p = 0.012$ )  
293 and maximum (total,  $p = 0.050$ ; annual,  $p = 0.025$ ) discharge during the year prior to vegetation sampling as  
294 well as with increasing mean (total,  $p = 0.045$ ; annual,  $p = 0.012$ ) discharge during the vegetation-growing  
295 season. For the upstream island, none of the correlations between hydrological conditions and richness patterns  
296 was significant. Regarding interannual variations in climatic conditions, only the total cumulative species  
297 richness decreased significantly with increasing total precipitation during the year prior to vegetation sampling  
298 ( $p = 0.050$ ).

### 299 **Changes in species composition between islands and from the 2012 baseline year**

300 Plant species composition differed significantly among islands ( $F_{2,87} = 23.09$ ,  $p = 0.001$ ) and years ( $F_{9,80} = 2.34$ ,  $p$   
301  $= 0.001$ ) (Figure 4-A). Pairwise comparisons showed that the plant composition varied significantly between all  
302 pairs of islands (Downstream-Rejuvenated,  $F_{1,58} = 23.68$ ,  $p\text{-adjust} = 0.001$ ; Downstream-Upstream,  $F_{1,58} = 12.56$ ,  
303  $p\text{-adjust} = 0.001$ ; Rejuvenated-Upstream,  $F_{1,58} = 28.15$ ,  $p\text{-adjust} = 0.001$ ). CAP ordination revealed that the  
304 composition of the rejuvenated island differed from the other two islands along axis 1, while the composition  
305 of the upstream and downstream islands differed along axis 2. Regarding the effect of time since fluvial  
306 maintenance works, i.e., 2012, pairwise comparisons revealed significant changes in species composition with  
307 the years 2013 ( $F_{1,16} = 3.84$ ,  $p\text{-adjust} = 0.009$ ), 2016 ( $F_{1,16} = 2.86$ ,  $p\text{-adjust} = 0.042$ ), 2017 ( $F_{1,16} = 4.17$ ,  $p\text{-adjust} =$   
308  $0.024$ ), 2018 ( $F_{1,16} = 4.07$ ,  $p\text{-adjust} = 0.030$ ) and 2019 ( $F_{1,16} = 5.68$ ,  $p\text{-adjust} = 0.009$ ). CAP ordination, however,  
309 showed that this effect was significant only for the rejuvenated island. Finally, the nestedness metric for the  
310 species-by-site matrix was significantly different from the simulated mean under the null model (NODF = 66.16,  
311  $p = 0.001$ ). This indicates that species-poor samples were a subset of species-rich samples and thus that the  
312 observed shift in species composition revealed by PERMANOVAs between islands and years was more likely the  
313 result of nestedness rather than species turnover.

314 The phi coefficient of association revealed that, among the 415 considered species (i.e., excluding 7 species  
315 only found in 2012), 55 species were associated with the downstream island, 9 species were associated with  
316 the rejuvenated island and 77 species were associated with the upstream island (Table 1 & Appendix S1). Of  
317 these, almost all species associated with the rejuvenated island were annuals or were pioneer species, such as

318 *Salix alba* in particular. Regarding the phi coefficient of association between years, 12 species were  
319 preferentially associated with the year 2014, 4 with the year 2015, one species with the year 2016, 12 species  
320 with the year 2017, 33 species with the year 2019, 4 species with the year 2020 and 2 species with the year  
321 2021. No species were preferentially associated with the years 2013 or 2018.

### 322 **Influence of interannual variations in hydrological and climatic conditions on species composition**

323 CAP ordination revealed that 8.9% ( $F_{4,84} = 5.08$ ,  $p = 0.001$ ) of the variation in species composition was explained  
324 by the two hydrological and the two climatic variables, after that the effect of species richness was removed  
325 from the analysis (Figure 4-B). The first CAP axis was negatively related to the mean (25.8%,  $p = 0.001$ ) and  
326 maximum discharge (17.3%,  $p = 0.001$ ) during the vegetation growing season. Based on species scores along  
327 this first CAP axis (Appendix S2), *Asparagus officinalis*, *Solidago gigantea* and *Galium album* (i.e., all perennial  
328 species) were the three species that were most negatively associated with years of high discharges, while  
329 *Panicum dichotomiflorum*, *Senecio vulgaris*, and *Helminthotheca echioides* (i.e., all annual species) were the  
330 three species that were most positively associated with years of high discharges. The second CAP axis was  
331 positively related to the mean temperature (30.8%,  $p = 0.001$ ) but negatively to total precipitation (26.1%,  $p =$   
332 0.003) during the vegetation growing season. Based on species scores along this second CAP axis, *Salix x*  
333 *rubens*, *Salix viminalis* and *Cyperus fuscus* were the three species that were most negatively associated with  
334 years characterized by warm and dry conditions, while *Persicaria mitis*, *Plantago arenaria* and *Fallopia*  
335 *dumetorum* were the three species that were most positively associated with years characterized by warm and  
336 dry conditions.

337

### 338 **DISCUSSION**

339 By implementing long-term vegetation monitoring, which is rarely done to evaluate the effects of restoration  
340 operations (González et al. 2015), we highlighted strong variations in diversity patterns in space and time.  
341 Specifically, we showed that artificial rejuvenation operations had a significant short-term negative effect on  
342 plant richness. Compared to the effect of floods recorded over the past 10 years, no combination of hydro-  
343 climatic conditions has resulted in such low levels of diversity. However, in just a few years, the communities  
344 have diversified and the species that have colonized the rejuvenated island, including numerous annuals, have  
345 contributed to increasing the species pool present throughout the island complex. Furthermore, although  
346 increased species richness in riparian ecosystems does not necessarily mean improved ecological status, our

347 results show that the works did not directly favor or hinder the establishment of heritage or undesirable  
348 species. Instead, we highlighted that changes in richness patterns over time, with the exception of undesirable  
349 species, were strongly determined by hydrological conditions, with a significant positive effect of spring and  
350 summer low flow for sandy gravel bar flora. Therefore, by recreating pioneer habitats exposed to flooding, the  
351 maintenance works have promoted the establishment of annual species-rich communities and triggered the  
352 regeneration of the pioneer tree *Salix alba*. From this view, and mostly because the other two islands used as  
353 control areas were in more advanced successional stages, it can be argued that the fluvial maintenance works  
354 in regulated rivers have the potential to increase the mosaic of habitats within the riverbed and thus promoted  
355 greater biodiversity. These results show that flood risk prevention measures do not necessarily conflict with  
356 conservation goals.

### 357 **Effects of the maintenance works on the richness and composition of riparian communities**

358 As expected, we found a strong decrease in species richness when comparing pre- and immediate post-works  
359 levels. Although a decrease in total richness was also noticeable on the downstream and upstream islands used  
360 as control areas between the 2012 and 2013 years, this effect was only significant on the rejuvenated island.  
361 Therefore, at the island complex scale, the temporary high loss in species found could be attributed to the  
362 maintenance works. Indeed, by removing all vegetation, including roots, and lowering the topographic levels,  
363 these works resulted in a total reset of the communities (Wintenberger et al. 2015). From this point of view, it  
364 can be argued that fluvial maintenance works had a strong negative impact in the short term on the ecological  
365 value of the riparian habitats (Shields & Nunnally 1984). Vegetation monitoring over a long period showed a  
366 gradual but non-linear increase in species richness on the rejuvenated island. Thus, five years after the  
367 completion of the works, the richness had returned to its initial (i.e., pre-treatment) level. However, the species  
368 richness of the rejuvenated island remains lower than that of the downstream and upstream islands. This is  
369 undoubtedly a direct effect of the works that, by homogenizing abiotic conditions across the island  
370 (Wintenberger et al. 2019), have constrained the expression of the hydrological gradient and the related  
371 environmental filtering and dispersal filtering processes (Fraaije et al. 2015) responsible for high turnover in  
372 riparian communities over small spatial scales. This lower diversity level is offset by the fact that the  
373 rejuvenated island contributes to the enrichment of the species pool by bringing in new species at the island  
374 complex scale (i.e., between 2013 and 2021, the number of unique species was 34 for the downstream island,  
375 42 for the rejuvenated island and 46 for the upstream island). Thus, from two to nine years after completion,

376 the species pool was almost always above the 2012 baseline year level. This indicates that rejuvenation  
377 operations, by increasing the connectivity of sandy gravel bar surfaces to river flows, have allowed the rapid  
378 colonization of partially different species (Moggridge et al. 2009; Geerling et al. 2008), including many annuals.  
379 Specifically, the constrained canonical analysis of principal coordinates showed that prior to maintenance  
380 works, the species composition on the rejuvenated island was close to that one of the upstream island, but  
381 after works, its position in the factorial space was clearly differentiated, thus revealing a shift in species  
382 composition. This shift was mainly due to the preferential presence of a few annual species characteristics of  
383 sandy gravel bars on the rejuvenated island, e.g., *Cyperus michelianus*, *Oxybasis glauca* and *Oxybasis rubra*.  
384 Among these species, some are considered heritage species and their presence in the Nature Reserve  
385 contributes to increasing the conservation value of the pioneer riparian habitats. Furthermore, our results  
386 showed that the new environmental conditions created on the rejuvenated island benefited *Salix alba*  
387 seedlings. The regeneration of this species have been greatly reduced on human-impacted rivers (González et  
388 al. 2018), due to its vulnerability to drought stress and shorter flood durations (Hortobágyi et al. 2018).  
389 Therefore, our results indicate that fluvial maintenance works have recreated a functional pioneer habitat that  
390 benefits early-successional species (Geerling et al. 2008; Friedman et al. 1995). Finally, although an increase in  
391 the richness of undesirable species was evidenced after the completion of the works, there is no evidence that  
392 it was directly related to maintenance operations. Indeed, our results showed that, at the scale of the three  
393 individual islands, undesirable species richness did not increase significantly. This indicates that each island has  
394 contributed a little to this pattern and thus that maintenance works have not favored the establishment of new  
395 undesirable species within the Nature Reserve. Rather, these results seem to indicate that the increase in the  
396 pool of undesirable species is most likely the result of external processes, linked to the arrival of new alien  
397 species in the upstream watershed of the Loire River. Thus, since the beginning of the vegetation surveys,  
398 several new undesirable species have been observed each year, e.g., *Erigeron sumatrensis*, *Paspalum distichum*  
399 and *Senecio inaequidens* in 2015, *Juglans nigra* in 2018 and *Azolla filiculoides* in 2019. This trend found at a  
400 local scale is consistent with global patterns showing an increase over time of alien species in ecosystems  
401 (Seebens et al. 2017), including in riparian environments (Richardson et al. 2007).

#### 402 **Effects of hydrological and climatic variations on the richness and composition of riparian communities**

403 Strong correlations were found between hydrological conditions and richness patterns. As previously  
404 evidenced in several studies (Pollock et al. 1998; Vervuren et al. 2003; Biswas & Mallik 2010), we have shown

405 that riparian species richness decreased with increasing flooding intensity, particularly during the season  
406 before vegetation development (Johansson & Nilsson 2002; van Eck et al. 2004; Antheunisse & Verhoeven  
407 2008). Despite the fact that we did not experience large floods during the 10 years of vegetation monitoring,  
408 the interannual variations of the mean discharge were strong enough to influence the total and annual plant  
409 richness as well as the richness of heritage species. Furthermore, although this effect was significant for all  
410 three islands studied, the strongest negative correlations ( $Rho < -0.8$ ) were found on the rejuvenated and  
411 downstream islands, with the most negative values observed for annual species. Indeed, compared to the  
412 upstream island, which is at a higher relative elevation from the waterline, these two islands had larger areas of  
413 sandbars exposed to flooding. Since the riparian communities established on the most connected fluvial  
414 landforms are more composed of annual species (Leyer 2006; Škornik et al. 2017; Greulich et al. 2019), which  
415 respond more directly to flood events (Nilsson et al. 1989; Greet et al. 2013; Kalníková et al. 2018), this may  
416 explain the strong correlation found and also the synchronous variations in richness patterns between these  
417 two islands over the last 10 years. However, over this monitoring period, the largest flood peak occurred in  
418 spring 2013, i.e., a few months after the completion of the rejuvenation works, implying that its effect on plant  
419 diversity was partially confounded with the maintenance works. The strong decrease in species richness  
420 observed directly in the year following maintenance operations is therefore related to the combined effects of  
421 works and flooding on the rejuvenated island. Moreover, because the reprofiling work led to the creation of a  
422 flat sandy gravel bar surface and lowered the relative elevation to the waterline (Wintenberger et al. 2015), the  
423 vulnerability of this island to small-magnitude flooding is higher compared to the other two islands. This may  
424 explain the 4-year lag time required to recover a level of diversity comparable to that before maintenance  
425 works. On the other hand, rejuvenation operations have clearly benefited annual species, with rapid  
426 colonization of sandbar areas beginning in 2014. Coupled with changes in hydrological conditions, the two  
427 peaks in biodiversity recorded in 2017 and 2019 at the scale of the island complex are therefore mainly related  
428 to the increase in annual species richness on the three islands studied. Indeed, respectively 81% and 72% of the  
429 species that were preferentially associated with the years 2017 and 2019 were annual species. As these two  
430 years were characterized by the lowest values of the mean and maximum discharges during the vegetation  
431 growing season, our results indicate that prolonged summer low water is very favorable to the expression of  
432 diversified communities (Greet et al. 2013), including many annuals characteristics of sandbars such as  
433 *Corrigiola littoralis*, *Cyperus fuscus*, *Persicaria lapathifolia* or *Portulaca granulatostellulata*. Combined with dry



434 and warm climatic conditions, as suggested by the results found on the rejuvenated island, it appears that the  
435 combination of these hydro-climatic conditions is very favorable to riparian biodiversity on the middle Loire.  
436 However, the strongest negative correlation ( $Rho < -0.7$ ) between cumulative richness of undesirable species  
437 and hydrological conditions (i.e., mean discharge during the growing season) was found on the rejuvenated  
438 island. This suggests that summer flooding primarily influenced alien species with annual life cycles and that  
439 perennial alien species are less sensitive to interannual variations in hydro-climatic conditions. Indeed, among  
440 the 44 undesirable species inventoried at the island complex scale, most of the perennial species were  
441 recorded on higher surface elevations, e.g., *Acer negundo*, *Reynoutria x bohemica*, *Robinia pseudoacacia*, while  
442 most of the annual species were recorded on lower surface elevations, e.g., *Ambrosia artemisiifolia*, *Bidens*  
443 *frondosa*, *Xanthium orientale*. Thus, potentially due to too few floods events over the 10-years of monitoring,  
444 our results do not show that flooding influences the prevalence of alien species (Thomaz 2021) but rather that  
445 once established, perennial species are stable over time, especially as they occupy vegetated islands with little  
446 connection to the river (Brummer et al. 2016). Taken together, our results show a strong response of riparian  
447 communities to interannual variations in hydrological conditions, particularly for the most exposed sandy  
448 gravel bar habitats rich in annuals species.

#### 449 **Research needs for the restoration of riparian pioneer communities**

450 Centuries of river engineering have profoundly altered the functionality of hydrosystems. By disconnecting  
451 floodplains from rivers, these developments have induced legacy effects that constrain the expression of  
452 hydrogeomorphic processes (e.g., Vauclin et al. 2020) and orient riparian communities toward more advanced  
453 successional stages (e.g., Janssen et al. 2020). Since the rejuvenation of alluvial habitats in regulated rivers is no  
454 longer assured by frequent floods of sufficient intensity to reshape the riverbed morphology (e.g., Geerling et  
455 al. 2006), it has been argued that management strategies are needed to restore more functional riparian  
456 habitats (Leyer 2006; Gerard et al. 2008). However, implementation of these management strategies must be  
457 based on sound empirical knowledge, as restoration outcomes may be conditioned by several local and  
458 regional biotic (e.g., species pool, degree of invasion of habitats by invasive alien species) and abiotic (e.g.,  
459 dynamic of disturbances, climate, soil characteristics) factors (e.g., Richardson et al. 2007; Baattrup-Pedersen  
460 et al. 2013). Thus, although the middle Loire case study showed that fluvial maintenance work benefited the  
461 pioneer communities by increasing the area of sandy gravel bar habitats, the generalization of these results  
462 should be done with caution. Indeed, because this study is not spatially replicated (i.e., limited to one

463 treatment and two controls), the response of plant communities in others rivers, e.g., with different valley  
464 geometry, may be different. Also, even if the Loire is regulated by a few dams that reduce the intensity of  
465 natural disturbances, it has a sandy-gravel bed with a high mobility of sediments, even for low levels of  
466 hydraulic constraints. In highly regulated and channelized gravel bed rivers, where flow and sediment regimes  
467 are largely altered but also where restoration of pioneer riparian communities is a major issue, as is the case  
468 for the Rhone (e.g., Janssen et al. 2021) and the Rhine (e.g., Baptist et al. 2004), there is an urgent need to  
469 better document the response and dynamics of riparian communities to artificially rejuvenated surfaces. From  
470 this perspective, our results highlight the need to study the individual response of structurally important  
471 species, such as *Salix alba*, but also of groups of species indicative of changes in habitat functioning, such as  
472 annual species, or in their conservation value, such as heritage species, to evaluate the success of restoration  
473 operations. Finally, our results emphasize the importance of long-term monitoring of vegetation after the  
474 completion of restoration actions, particularly for riparian environments subject to significant interannual  
475 variation in disturbance regime (González et al. 2015; England et al. 2021). This will both provide a better  
476 understanding of the successional trajectories of riparian communities on newly recreated geomorphic  
477 surfaces, but also how seasonal and interannual variations in flow shape communities over time and thus the  
478 levels of disturbance necessary to maintain functional pioneer habitats.

479

#### 480 **ACKNOWLEDGEMENTS**

481 We thank Noémie Bertrand, Ophélie Beslin, Aurélie Bouvet, Adélie Chevalier, Nicolas Déjean, Florient  
482 Desmoulins, Agnès Hergibo, Philippe Jugé, Félix Langlois, Martin Marchand, Jeanne Menanteau, Pierre Payan,  
483 Coryse Pernet, Emmanuel Pineau, Sara Robert and Anne Villemey for help in the field. This work was cofunded  
484 by the Région Centre-Val de Loire and the European Union (Feder N° PRESAGE 37729 and Feder 2016-  
485 EX00604), through BioMareau and BioMareau-II research projects. European Union is engaged on the Loire  
486 Basin with the European regional development fund (ERDF). We also thank the "Direction Départementale du  
487 Territoire, Service Loire, risques, transports (Pôle Loire) " which, as project manager on behalf of the state,  
488 conducted the clearing and lowering of the topographic level, in 2012, following the recommendations of the  
489 BioMareau research team.

490

#### 491 **REFERENCES**

492 Almeida-Neto M, Guimaraes P, Guimarães PR, Loyola RD, Ulrich W (2008) A consistent metric for nestedness  
493 analysis in ecological systems: reconciling concept and measurement. *Oikos* 117:1227–1239

494 Anderson MJ, Willis TJ (2003) Canonical analysis of principal coordinates: a useful method of constrained  
495 ordination for ecology. *Ecology* 84:511–525

496 Antheunisse AM, Verhoeven JTA (2008) Short-term responses of soil nutrient dynamics and herbaceous  
497 riverine plant communities to summer inundation. *Wetlands* 28:232–244

498 Baattrup-Pedersen A, Dalkvist D, Dybkjaer JB, Riis T, Larsen SE, Kronvang B (2013) Species recruitment following  
499 flooding, sediment deposition and seed addition in restored riparian areas. *Restoration Ecology*  
500 21:399–408

501 Baptist MJ, Penning WE, Duel H, Smits AJM, Geerling GW, Van Der Lee GEM, Van Alphen JSM (2004)  
502 Assessment of the effects of cyclic floodplain rejuvenation on flood levels and biodiversity along the  
503 Rhine River. *River Research and Applications* 20:285–297

504 Biswas SR, Mallik AU (2010) Disturbance effects on species diversity and functional diversity in riparian and  
505 upland plant communities. *Ecology* 91:28–35

506 Brummer TJ, Byrom AE, Sullivan JJ, Hulme PE (2016) Alien and native plant richness and abundance respond to  
507 different environmental drivers across multiple gravel floodplain ecosystems. *Diversity and*  
508 *Distributions* 22:823–835

509 Burnouf J, Carcaud N, Garcin M (2009) Nouvelle histoire pour la Loire entre nature et société. *Géosciences*  
510 9:72–79

511 Caponi F, Koch A, Bertoldi W, Vetsch DF, Siviglia A (2019) When does vegetation establish on gravel bars?  
512 Observations and modeling in the alpine Rhine River. *Frontiers in Environmental Science* 7:1–18

513 Catlin DH, Fraser JD, Felio JH (2015) Demographic responses of piping plovers to habitat creation on the  
514 Missouri river: Piping Plover Population Dynamics. *Wildlife Monographs* 192:1–42

515 Chevalier R, Gautier G, Archaux F (2010) Relevés floristiques pour le suivi de la biodiversité végétale des  
516 écosystèmes forestiers : éléments de réflexion pour faire les bons choix. *Revue Forestière Française*  
517 LXII:141–154

518 Cordier J, Filoche S (2016) Notice du catalogue de la flore vasculaire du Centre-Val de Loire. Version mai 2016.  
519 Conservatoire botanique national du Bassin parisien, Paris

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

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

527 De Cáceres M, Legendre P (2009) Associations between species and groups of sites: indices and statistical  
528 inference. *Ecology* 90:3566–3574

529 Desmoulins F, Emeriau T (2017) Liste des espèces végétales invasives du Centre-Val de Loire, version 3.0.  
530 Conservatoire botanique national du Bassin parisien, délégation Centre-Val de Loire

531 Dudgeon D, Arthington AH, Gessner MO, Kawabata Z-I, Knowler DJ, Lévêque C, Naiman RJ, Prieur-Richard A-H,  
532 Soto D, Stiassny MLJ, Sullivan CA (2006) Freshwater biodiversity: importance, threats, status and  
533 conservation challenges. *Biological Reviews* 81:163–182

534 van Eck WHJM, van de Steeg HM, Blom CWPM, de Kroon H (2004) Is tolerance to summer flooding correlated  
535 with distribution patterns in river floodplains? A comparative study of 20 terrestrial grassland species.  
536 *Oikos* 107:393–405

537 Egger G, Politti E, Lautsch E, Benjankar R, Gill KM, Rood SB (2015) Floodplain forest succession reveals fluvial  
538 processes: A hydrogeomorphic model for temperate riparian woodlands. *Journal of Environmental*  
539 *Management* 161:72–82

540 England J, Angelopoulos N, Cooksley S, Dodd J, Gill A, Gilvear D, Johnson M, Naura M, O'Hare M, Tree A,  
541 Wheeldon J, Wilkes MA (2021) Best practices for monitoring and assessing the ecological response to  
542 river restoration. *Water* 13:3352

543 Fraaije RGA, Braak CJF, Verduyn B, Verhoeven JTA, Soons MB (2015) Dispersal *versus* environmental filtering in  
544 a dynamic system: drivers of vegetation patterns and diversity along stream riparian gradients. *Journal*  
545 *of Ecology* 103:1634–1646

546 Friedman JM, Scott ML, Lewis WM (1995) Restoration of riparian forest using irrigation, artificial disturbance,  
547 and natural seedfall. *Environmental Management* 19:547–557

548 Gann GD, McDonald T, Walder B, Aronson J, Nelson CR, Jonson J, Hallett JG, Eisenberg C, Guariguata MR, Liu J,  
549 Hua F, Echeverría C, Gonzales E, Shaw N, Decler K, Dixon KW (2019) International principles and  
550 standards for the practice of ecological restoration. Second edition. *Restoration Ecology* 27:S1–S46

551 Geerling GW, Kater E, van den Brink C, Baptist MJ, Ragas AMJ, Smits AJM (2008) Nature rehabilitation by  
552 floodplain excavation: The hydraulic effect of 16 years of sedimentation and vegetation succession  
553 along the Waal River, NL. *Geomorphology* 99:317–328

554 Geerling GW, Ragas AMJ, Leuven RSEW, van den Berg JH, Breedveld M, Liefhebber D, Smits AJM (2006)  
555 Succession and rejuvenation in floodplains along the River Allier (France). *Hydrobiologia* 565:71–86

556 Gerard M, El Kahloun M, Rymen J, Beauchard O, Meire P (2008) Importance of mowing and flood frequency in  
557 promoting species richness in restored floodplains. *Journal of Applied Ecology* 45:1780–1789

558 González E, Martínez-Fernández V, Shafroth PB, Sher AA, Henry AL, Garófano-Gómez V, Corenblit D (2018)  
559 Regeneration of Salicaceae riparian forests in the Northern Hemisphere: A new framework and  
560 management tool. *Journal of Environmental Management* 218:374–387

561 González E, Sher AA, Tabacchi E, Masip A, Poulin M (2015) Restoration of riparian vegetation: A global review of  
562 implementation and evaluation approaches in the international, peer-reviewed literature. *Journal of*  
563 *Environmental Management* 158:85–94

564 Greet J, Cousens RD, Webb JA (2013) Seasonal timing of inundation affects riparian plant growth and flowering:  
565 implications for riparian vegetation composition. *Plant Ecology* 214:87–101

566 Greulich S, Chevalier R, Villar M (2019) Soil seed banks in the floodplain of a large river: A test of hypotheses on  
567 seed bank composition in relation to flooding and established vegetation. *Journal of Vegetation*  
568 *Science* 30:732–745

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

572 Gurnell AM, Petts GE, Hannah DM, Smith BPG, Edwards PJ, Kollmann J, Ward JV, Tockner K (2001) Riparian  
573 vegetation and island formation along the gravel-bed Fiume Tagliamento, Italy. *Earth Surface*  
574 *Processes and Landforms* 26:31–62

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

578 Janssen P, Stella JC, Piégay H, Räßple B, Pont B, Faton J-M, Cornelissen JHC, Evette A (2020) Divergence of  
579 riparian forest composition and functional traits from natural succession along a degraded river with  
580 multiple stressor legacies. *Science of the Total Environment* 721:137730

581 Janssen P, Stella JC, Räßple B, Gruel C-R, Seignemartin G, Pont B, Dufour S, Piégay H (2021) Long-term river  
582 management legacies strongly alter riparian forest attributes and constrain restoration strategies  
583 along a large, multi-use river. *Journal of Environmental Management* 279:111630

584 Johansson ME, Nilsson C (2002) Responses of riparian plants to flooding in free-flowing and regulated boreal  
585 rivers: an experimental study. *Journal of Applied Ecology* 39:971–986

586 Junk WJ, Bayley PB, Sparks RE (1989) The flood pulse concept in river-floodplain systems. *Canadian Special*  
587 *Publication of Fisheries and Aquatic Sciences* 106:110–127

588 Kalníková V, Chytrý K, Chytrý M (2018) Early vegetation succession on gravel bars of Czech Carpathian streams.  
589 *Folia Geobotanica* 53:317–332

590 Leyer I (2006) Dispersal, diversity and distribution patterns in pioneer vegetation: The role of river-floodplain  
591 connectivity. *Journal of Vegetation Science* 17:407–416

592 Méheust A, Varray S (2020) Liste hiérarchisée des espèces exotiques envahissantes du bassin Loire-Bretagne -  
593 version décembre 2020. Fédération des Conservatoires d'espaces naturels

594 Moggridge HL, Gurnell AM, Mountford JO (2009) Propagule input, transport and deposition in riparian  
595 environments: the importance of connectivity for diversity. *Journal of Vegetation Science* 20:465–474

596 Muñoz-Mas R, Garófano-Gómez V, Andrés-Doménech I, Corenblit D, Egger G, Francés F, Ferreira MT, García-  
597 Arias A, Politti E, Rivaes R, Rodríguez-González PM, Steiger J, Vallés-Morán FJ, Martínez-Capel F (2017)  
598 Exploring the key drivers of riparian woodland successional pathways across three European river  
599 reaches. *Ecohydrology* 10:e1888

600 Naiman RJ, Decamps H (1997) The ecology of interfaces: riparian zones. *Annual review of Ecology and*  
601 *Systematics* 28:621–658

602 Nilsson C, Grelsson G, Johansson M, Sperens U (1989) Patterns of plant species richness along riverbanks.  
603 *Ecology* 70:77–84

604 Oksanen J, Blanchet GF, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH,  
605 Wagner H (2013) *vegan: Community Ecology Package*. R package version 2.0-10.

606 Olden JD, Rooney TP (2006) On defining and quantifying biotic homogenization. *Global Ecology and*  
607 *Biogeography* 15:113–120

608 Planty-Tabacchi A-M, Tabacchi E, Naiman RJ, Deferrari C, Decamps H (1996) Invasibility of species-rich  
609 communities in riparian zones. *Conservation Biology* 10:598–607

610 Poff NL, Allan JD, Bain MB, Karr JR, Prestegard KL, Richter BD, Sparks RE, Stromberg JC (1997) The natural flow  
611 regime. *BioScience* 47:769–784

612 Pollock MM, Naiman RJ, Hanley TA (1998) Plant species richness in riparian wetlands - A test of biodiversity  
613 theory. *Ecology* 79:94–105

614 Polzin ML, Rood SB (2006) Effective disturbance: Seedling safe sites and patch recruitment of riparian  
615 cottonwoods after a major flood of a mountain river. *Wetlands* 26:965–980

616 R Core Team (2020) R: A language and environment for statistical computing. R Foundation for Statistical  
617 Computing, Vienna, Austria

618 Raunkiaer C (1934) The life forms of plants and statistical plant geography. Oxford University Press. Oxford  
619 University Press, Oxford, UK

620 Richardson DM, Holmes PM, Esler KJ, Galatowitsch SM, Stromberg JC, Kirkman SP, Pyšek P, Hobbs RJ (2007)  
621 Riparian vegetation: degradation, alien plant invasions, and restoration prospects. *Diversity and*  
622 *distributions* 13:126–139

623 Rossi J-P (2011) rich: An R Package to Analyse Species Richness. *Diversity* 3:112–120

624 Rottenborn J, Vítovcová K, Prach K (2018) Interannual dynamics of a rare vegetation on emerged river gravels  
625 with special attention to the critically endangered species *Corrigiola litoralis* L. *Folia Geobotanica*  
626 53:213–225

627 Seebens H, Blackburn TM, Dyer EE, Genovesi P, Hulme PE, Jeschke JM, Pagad S, Pyšek P, Winter M, Arianoutsou  
628 M, Bacher S, Blasius B, Brundu G, Capinha C, Celesti-Gradow L, Dawson W, Dullinger S, Fuentes N,  
629 Jäger H, Kartesz J, Kenis M, Kreft H, Kühn I, Lenzner B, Liebhold A, Mosena A, Moser D, Nishino M,  
630 Pearman D, Pergl J, Rabitsch W, Rojas-Sandoval J, Roques A, Rorke S, Rossinelli S, Roy HE, Scalera R,  
631 Schindler S, Štajerová K, Tokarska-Guzik B, van Kleunen M, Walker K, Weigelt P, Yamanaka T, Essl F  
632 (2017) No saturation in the accumulation of alien species worldwide. *Nature Communications* 8:14435

633 Shields FD, Nunnally NR (1984) Environmental aspects of clearing and snagging. *Journal of Environmental*  
634 *Engineering* 110:152–165



- 635 Škornik S, Meznarič M, Kaligarič M (2017) Factors affecting composition of gravel bar vegetation in middle  
636 reach of a lowland river. *Polish Journal of Ecology* 65:194–210
- 637 Tabacchi E, Planty-Tabacchi A-M, Salinas MJ, Décamps H (1996) Landscape structure and diversity in riparian  
638 plant communities: a longitudinal comparative study. *Regulated Rivers: Research & Management*  
639 12:367–390
- 640 Thomaz SM (2021) Propagule pressure and environmental filters related to non-native species success in river-  
641 floodplain ecosystems. *Hydrobiologia*
- 642 Tracy-Smith E, Galat DL, Jacobson RB (2012) Effects of flow dynamics on the aquatic-terrestrial transition zone  
643 (ATTZ) of the lower Missouri River sand bars with implications for selected biota. *River Research and*  
644 *Applications* 28:793–813
- 645 Ulrich W, Almeida-Neto M, Gotelli NJ (2009) A consumer's guide to nestedness analysis. *Oikos* 118:3–17
- 646 Vargas-Luna A, Crosato A, Uijttewaal WSJ (2015) Effects of vegetation on flow and sediment transport:  
647 comparative analyses and validation of predicting models. *Earth Surface Processes and Landforms*  
648 40:157–176
- 649 Vauclin S, Mourier B, Piégay H, Winiarski T (2020) Legacy sediments in a European context: The example of  
650 infrastructure-induced sediments on the Rhône River. *Anthropocene* 31:100248
- 651 Vervuren PJA, Blom CWPM, de Kroon H (2003) Extreme flooding events on the Rhine and the survival and  
652 distribution of riparian plant species. *Journal of Ecology* 91:135–146
- 653 Ward JV, Stanford JA (1995) Ecological connectivity in alluvial river ecosystems and its disruption by flow  
654 regulation. *Regulated Rivers: Research & Management* 11:105–119
- 655 Ward JV, Tockner K, Schiemer F (1999) Biodiversity of floodplain river ecosystems: ecotones and connectivity.  
656 *Regulated Rivers: Research & Management* 15:125–139

657 Wilkes MA, Gittins JR, Mathers KL, Mason R, Casas-Mulet R, Vanzo D, Mckenzie M, Murray-Bligh J, England J,  
658 Gurnell A, Jones JI (2019) Physical and biological controls on fine sediment transport and storage in  
659 rivers. *Wiley Interdisciplinary Reviews: Water* 6:e1331

660 Wintenberger CL, Rodrigues S, Claude N, Jugé P, Bréhéret J-G, Villar M (2015) Dynamics of nonmigrating mid-  
661 channel bar and superimposed dunes in a sandy-gravelly river (Loire River, France). *Geomorphology*  
662 248:185–204

663 Wintenberger CL, Rodrigues S, Greulich S, Bréhéret JG, Jugé P, Tal M, Dubois A, Villar M (2019) Control of non-  
664 migrating bar morphodynamics on survival of *Populus nigra* seedlings during floods. *Wetlands* 39:275–  
665 290

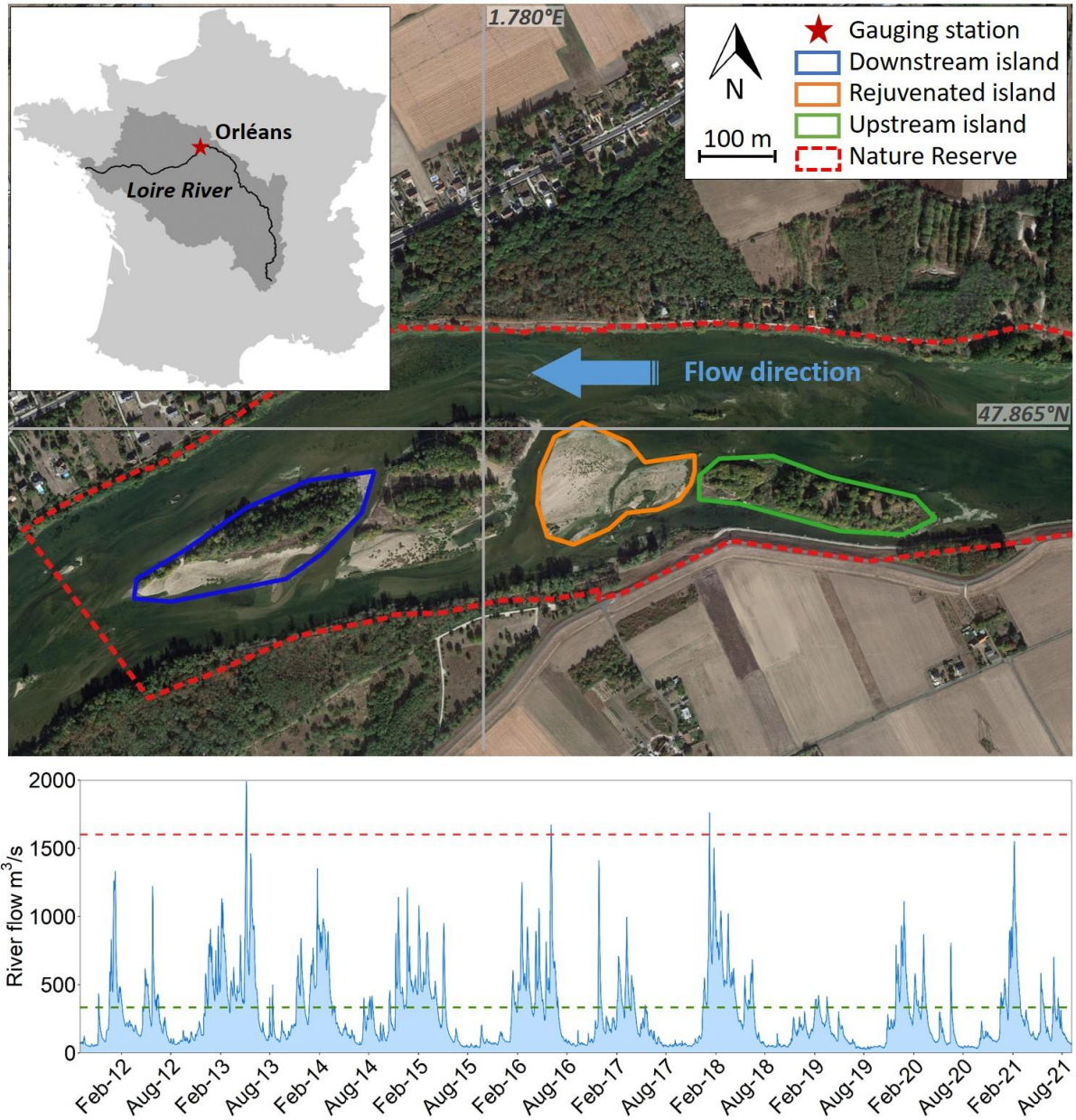
666

667 **Table 1.** Number of species more closely associated with any of the three islands or any of the nine years after  
668 fluvial maintenance works were completed, based on the phi coefficient of association (Loire River, France). For  
669 each island and year, the three species with the highest phi coefficient are provided when possible (+ = annual  
670 species, \* = undesirable species, underlined = heritage species, - = no association).

	Factor	Total	Annual	Heritage	Undesir.	Species
Island	Downstream	53	13	5	6	<i>Inula britannica</i> , <i>Paspalum distichum</i> *, <i>Schedonorus giganteus</i>
	Rejuvenated	11	7	3	1	<i>Chondrilla juncea</i> , <i>Salix alba</i> , <i>Rumex acetosella</i>
	Upstream	76	14	8	5	<i>Phragmites australis</i> , <i>Asparagus officinalis</i> , <i>Salix x rubens</i>
Year	2013	-	-	-	-	
	2014	12	8	4	2	<i>Impatiens glandulifera</i> *+, <i>Triticum sp</i> *+, <u><i>Centaurea stoebe</i></u>
	2015	4	1	1	-	<i>Helosciadium nodiflorum</i> , <i>Arctium minus</i> , <u><i>Dysphania botrys</i></u> +
	2016	1	-	-	1	<i>Egeria densa</i> *
	2017	11	9	1	1	<i>Oxalis dillenii</i> , <u><i>Oxybasis glauca</i></u> +, <i>Bidens tripartita</i> +
	2018	-	-	-	-	
	2019	33	24	1	9	<i>Papaver rhoeas</i> +, <i>Vulpia myuros</i> +, <i>Filago germanica</i> +
	2020	4	2	-	1	<i>Hypericum perforatum</i> , <i>Ludwigia grandiflora</i> *, <i>Torilis japonica</i> +
	2021	2	1	-	-	<i>Cynodon dactylon</i> , <i>Fallopia dumetorum</i> +

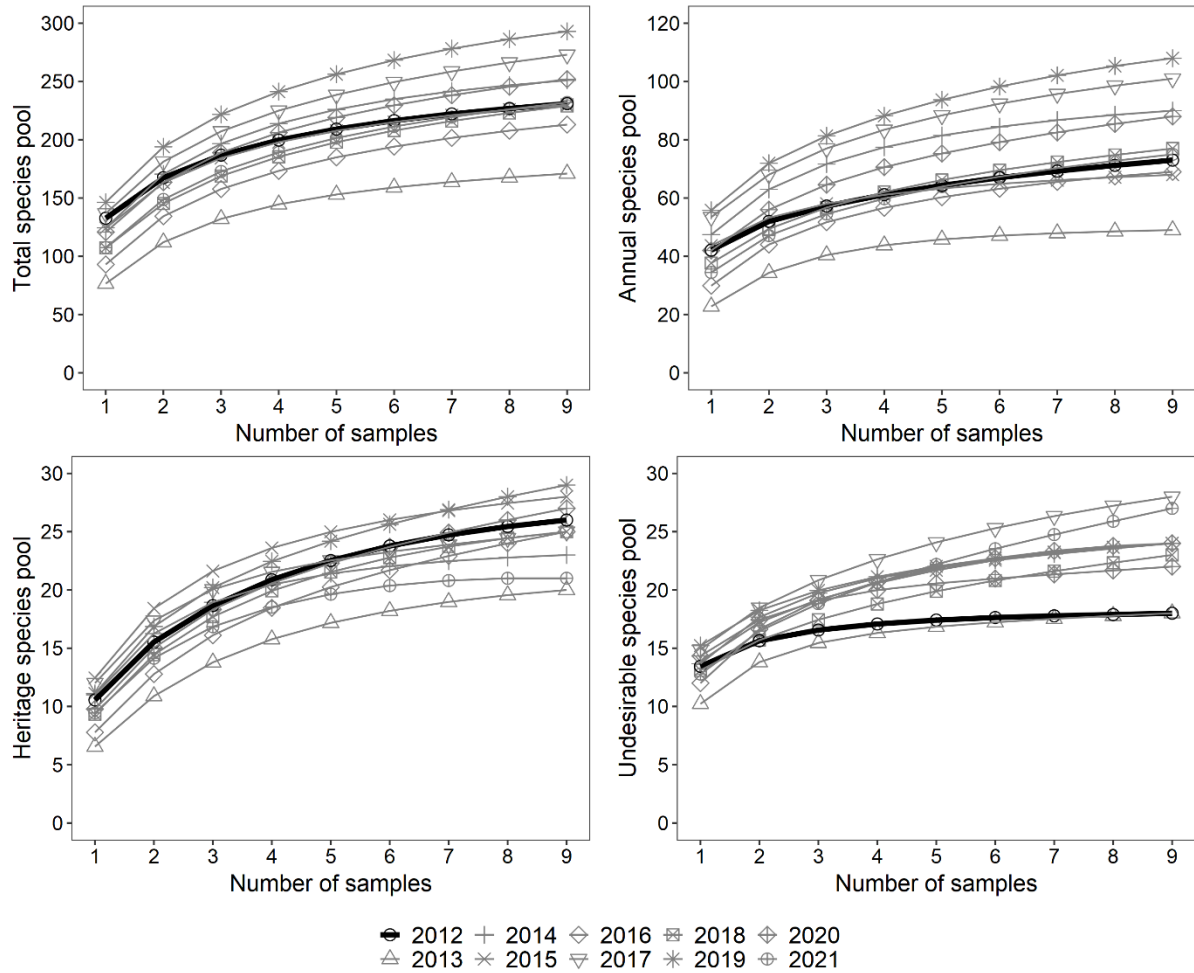
671

672 **Figure 1.** Location of the study area within the Loire River watershed, distribution of sampled islands within the  
 673 Loire River bed and flow regime variations over the last 10 years at the Pont Royal gauging station, in the city

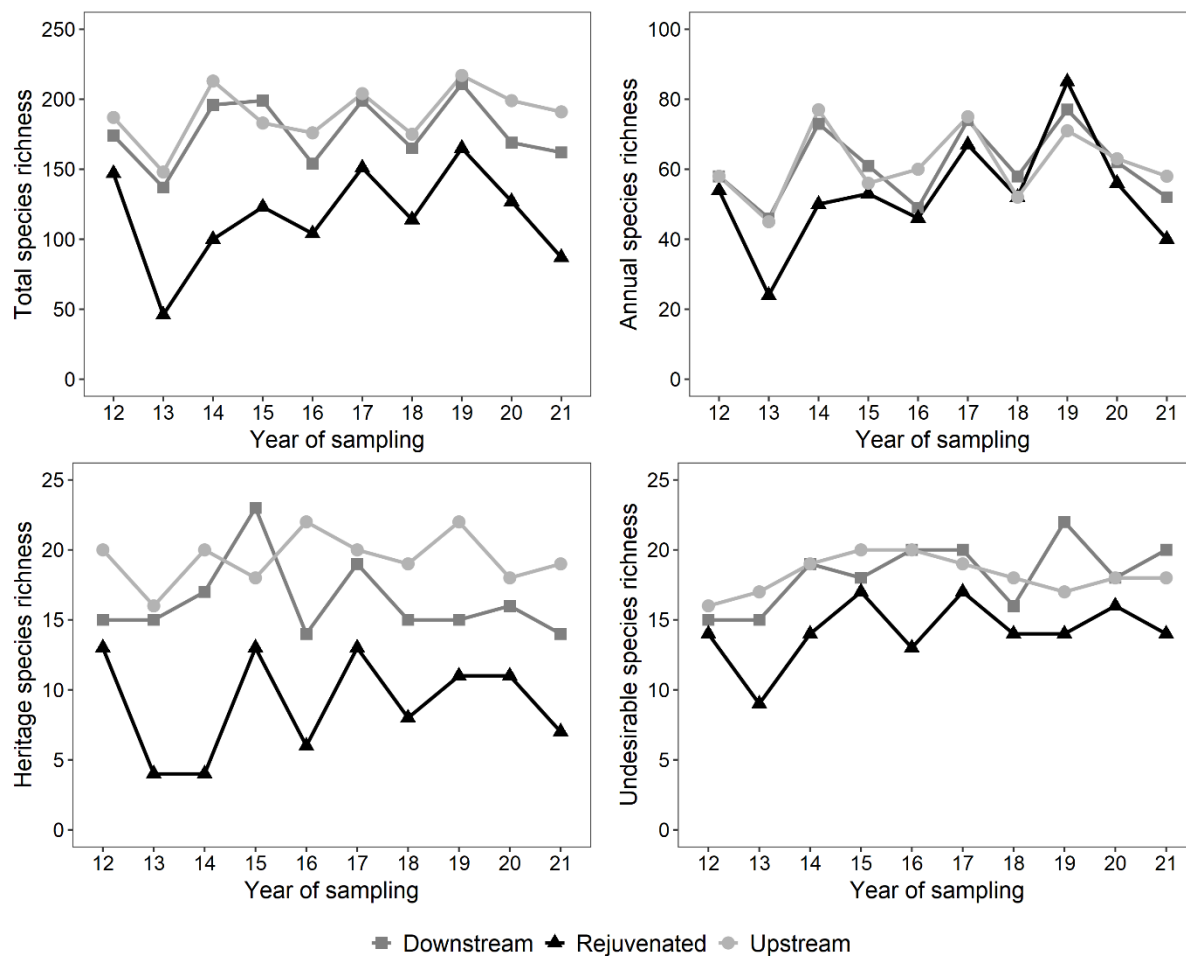


674 center of Orléans (dashed green line = interannual mean discharge; dashed red line = 2-year flood).

675 **Figure 2.** Species accumulation curves for comparing the cumulative richness of total, annual, heritage and  
 676 undesirable plant species on the island complex studied (Loire River, France). To facilitate comparison between  
 677 the baseline year (2012) and the 9 years following fluvial maintenance works (2013-2021), the associated  
 678 accumulation curve is shown in black (see Table S3 for detailed results).



679 **Figure 3.** Variations in cumulative species richness of total, annual, heritage and undesirable plant species  
 680 between years for each island studied (Loire River, France) (see Table S3 for detailed results).



681 **Figure 4.** Constrained canonical analysis of principal coordinates of riparian plant communities A) for each  
 682 island and year of vegetation monitoring and B) in relation to hydrological and climatic variables (Loire River,  
 683 France). To facilitate graphical interpretation, the centroids of each year for each island are represented by  
 684 connected lines and a number corresponding to the year of the vegetation survey is provided (e.g., 12 = 2012).  
 685 Species centroids for the three lowest and the three highest values along each axis are also provided: Amar\_blit  
 686 = *Amaranthus blitum*, Aris\_clem = *Aristolochia clematitis*, Aspa\_offi = *Asparagus officinalis*, Chon\_junc =  
 687 *Chondrilla juncea*, Cype\_fusc = *Cyperus fuscus*, Fall\_dume = *Fallopia dumetorum*, Gali\_albu = *Galium album*,  
 688 Helm\_echi = *Helminthotheca echioides*, Humu\_lupu = *Humulus lupulus*, Inul\_brit = *Inula Britannica*, Pani\_dich =  
 689 *Panicum dichotomiflorum*, Part\_inse = *Parthenocissus inserta*, Pasp\_dist = *Paspalum distichum*, Pers\_miti =  
 690 *Persicaria mitis*, Phra\_aust = *Phragmites australis*, Plan\_aren = *Plantago arenaria*, Rosa\_cani = *Rosa canina*,  
 691 Rume\_thyr = *Rumex thyriflorus*, Sali\_rube = *Salix x rubens*, Sali\_vimi = *Salix viminalis*, Sche\_giga = *Schedonorus*  
 692 *giganteus*, Sene\_vulg = *Senecio vulgaris*, Soli\_giga = *Solidago gigantea*.

