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)**

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

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ABSTRACT

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

IMPLICATIONS FOR PRACTICE:

- Clearing operations, if accompanied by a lowering of the topographic level of alluvial bars, can benefit pioneer riparian plant communities and thus be viewed as a means of assisting in the restoration of regulated rivers with vegetation encroachment
- The lowering of the topographic level must be done in such a way as to promote a greater frequency 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

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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 km²) in its

139 middle reach (mean annual discharge = 365 m^3/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

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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 occured after

168 the maintenance works (Wintenberger et al. 2015). In 2013, the typical longitudinal grain size fining

169 characterizing alluvial bars was observed iditenfying 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 crossed-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 km², mean annual discharge = 1 m^3/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 woks, 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 environemental

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 beween 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-adjust = 0.001; Downstream-Upstream, $F_{1,58}$ = 12.56,

303 p-adjust = 0.001; Rejuvenated-Upstream, $F_{1,58}$ = 28.15, p-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-adjust = 0.009), 2016 ($F_{1,16}$ = 2.86, p-adjust = 0.042), 2017 ($F_{1,16}$ = 4.17, p-adjust =

308 0.024), 2018 ($F_{1,16}$ = 4.07, p-adjust = 0.030) and 2019 ($F_{1,16}$ = 5.68, p-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

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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,

13

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, athough 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.

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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).

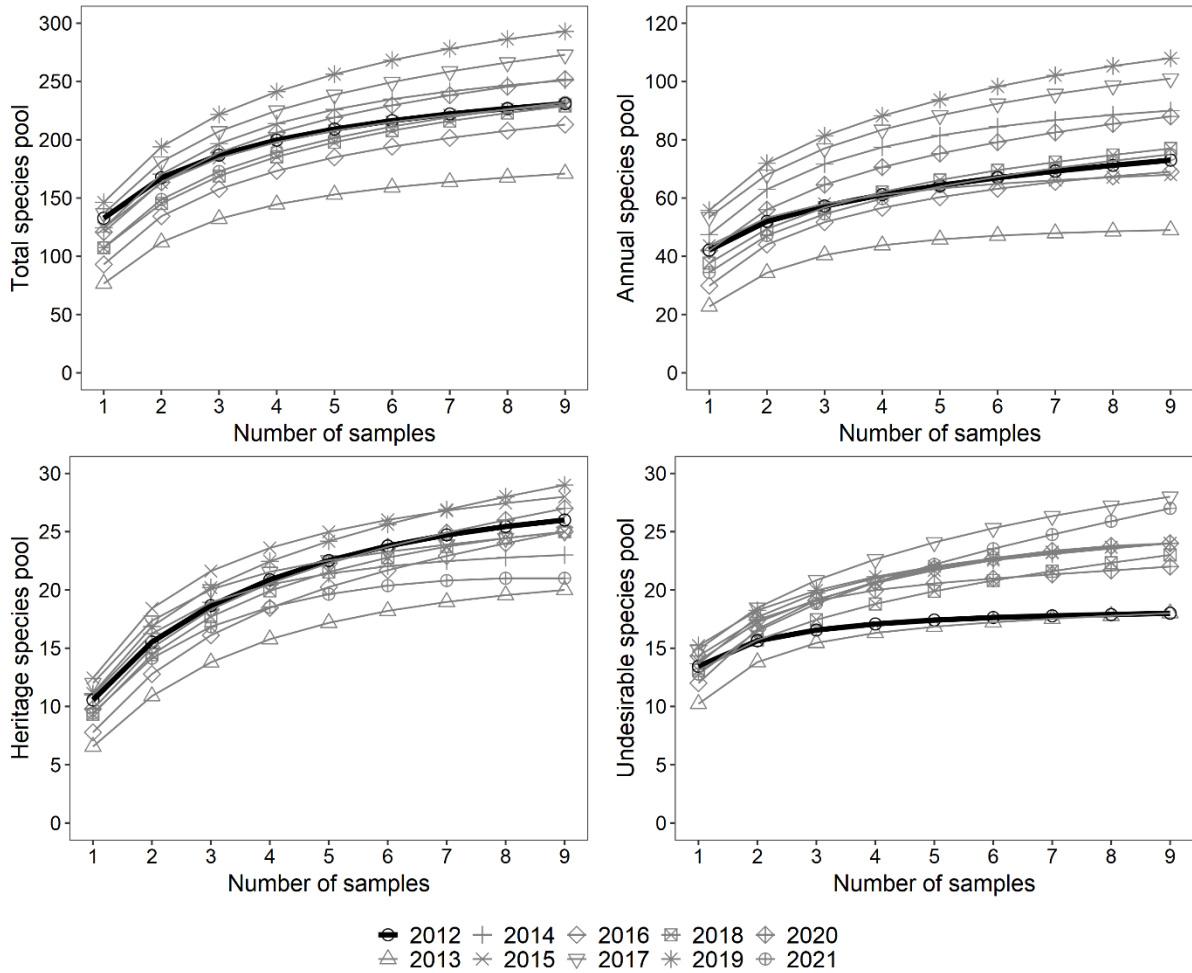|	Factor	Total	Annual	Heritage	Undesir.	Species
Island	Downstream	53	13	5	6	*Inula britannica, Paspalum distichum*, Schedonorus giganteus*
	Rejuvenated	11	7	3	1	*Chondrilla juncea, Salix alba, Rumex acetosella*
	Upstream	76	14	8	5	*Phragmites australis, Asparagus officinalis, Salix x rubens*
Year	2013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

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
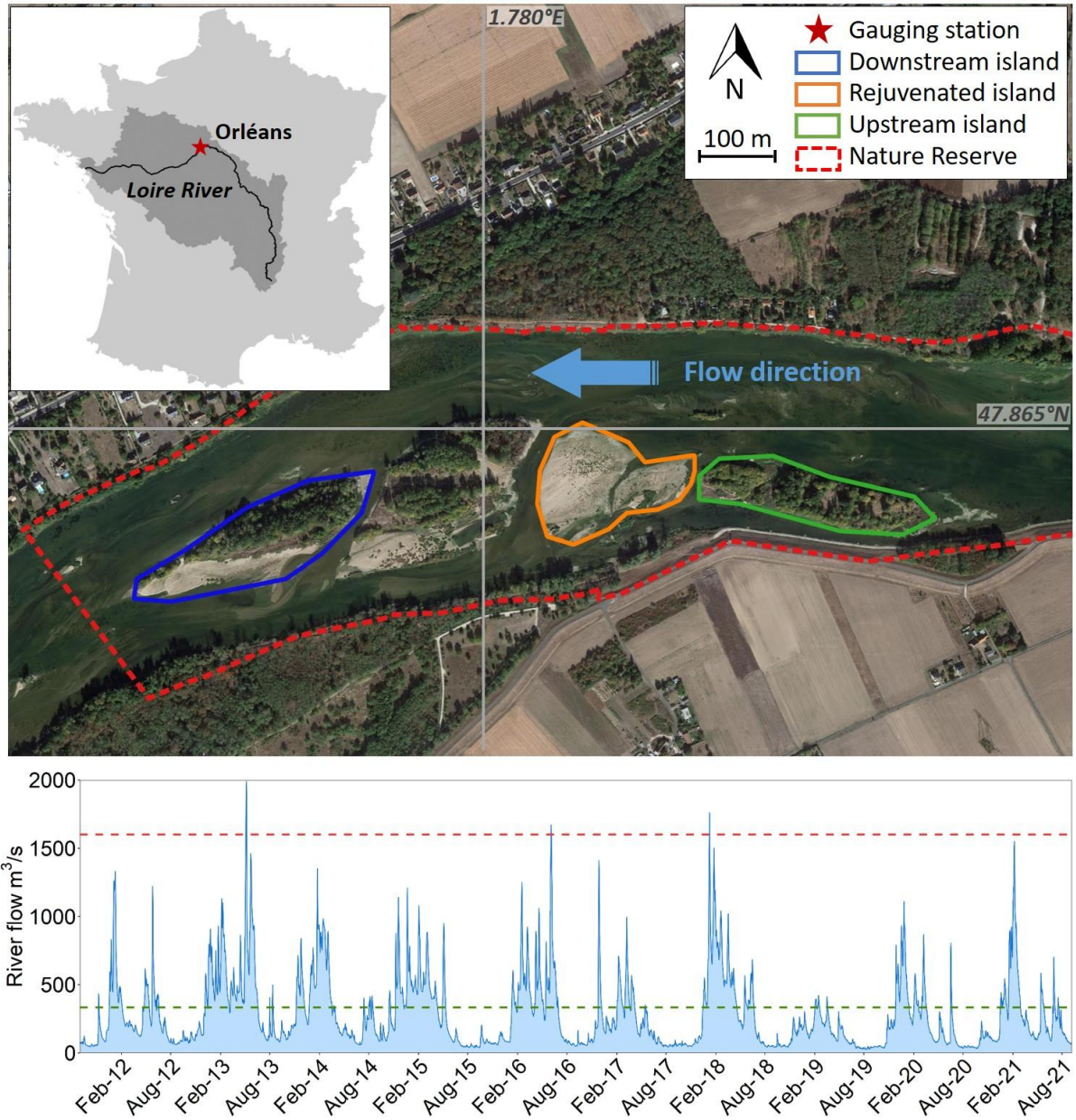

674 center of Orléans (dashed green line = interannual mean discharge; dashed red line = 2-year flood).

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).

Figure 3. Variations in cumulative species richness of total, annual, heritage and undesirable plant species

between years for each island studied (Loire River, France) (see Table S3 for detailed results).
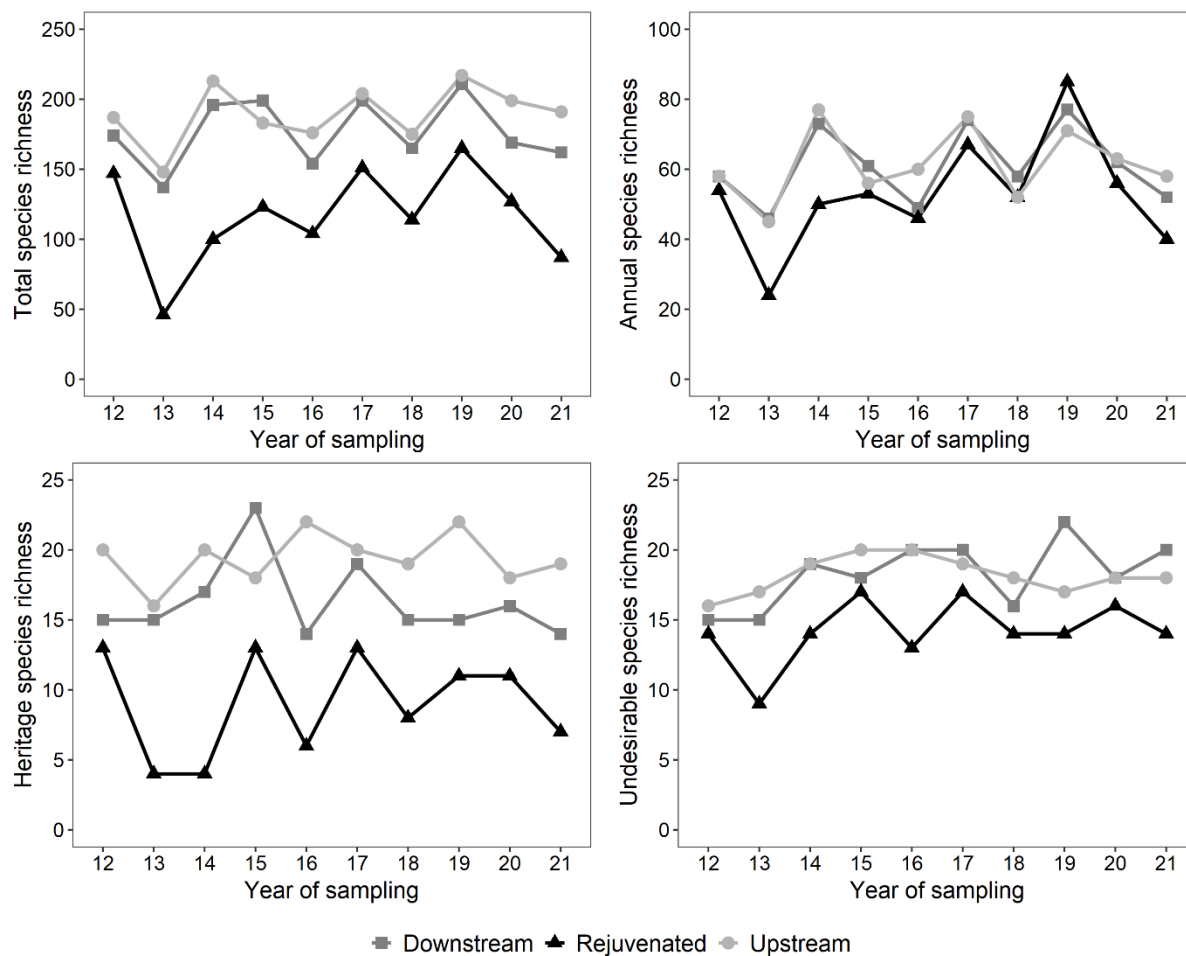
Figure 4. Constrained canonical analysis of principal coordinates of riparian plant communities A) for each island and year of vegetation monitoring and B) in relation to hydrological and climatic variables (Loire River, France). To facilitate graphical interpretation, the centroids of each year for each island are represented by connected lines and a number corresponding to the year of the vegetation survey is provided (e.g., 12 = 2012). Species centroids for the three lowest and the three higest values along each axis are also provided: Amar_blit = *Amaranthus blitum*, Aris_clem = *Aristolochia clematitis*, Aspa_offi = *Asparagus officinalis,* Chon_junc = *Chondrilla juncea*, Cype_fusc = *Cyperus fuscus,* Fall_dume = *Fallopia dumetorum,* Gali_albu = Galium album, Helm_echi = *Helminthotheca echioides,* Humu_lupu = *Humulus lupulus*, Inul_brit = *Inula Britannica*, Pani_dich = *Panicum dichotomiflorum*, Part_inse = *Parthenocissus inserta*, Pasp_dist = *Paspalum distichum*, Pers_miti = *Persicaria mitis*, Phra_aust = *Phragmites australis*, Plan_aren = *Plantago arenaria,* Rosa_cani = *Rosa canina*, Rume_thyr = *Rumex thyrsiflorus*, Sali_rube = *Salix* x *rubens,* Sali_vimi = *Salix viminalis,* Sche_giga = *Schedonorus giganteus*, Sene_vulg = *Senecio vulgaris*, Soli_giga = *Solidago gigantea.*