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1 **The taxonomic structure but not the functioning of riparian herbaceous communities varies with**  
2 **hydrological conditions on a large, highly regulated river: evidence from a two-year replicated study**

3

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13

14 Short title: Spatiotemporal variations of riparian communities in a regulated river

15 Keywords: Gravel bar, Inundation, Plant traits, Rhône River, Riverine vegetation

16 **ABSTRACT**

17 Riparian vegetation encompasses dynamic communities structured by strong environmental gradients. Due to  
18 anthropogenic changes, a greater uniformity of environmental conditions is observed along local gradients. To  
19 maintain diverse and functional communities in regulated rivers, there is an urgent need to finely characterize  
20 the factors controlling the spatial and temporal dynamics of riparian vegetation. In the summer of 2017 and  
21 2019, we repeatedly sampled 8 gravel bars along the regulated Rhône River. Using a taxonomic and functional  
22 approach, we assessed whether the diversity and composition of species and traits varied between the two  
23 years at the corridor and site scales. Taxonomic diversity decreased and composition changed between years,  
24 while functional diversity and composition did not. Specifically, we showed that variation in taxonomic diversity  
25 was largely limited to species sharing the same trait values, suggesting some functional resilience of riparian  
26 communities to environmental changes. In addition, we found that changes between the two years concerned  
27 primarily the communities established on low-lying bars made up of coarse-grained sediments, more  
28 frequently and intensely inundated. Beyond being the most responsive to environmental changes, these  
29 riparian communities were also the most diverse in species and trait values. However, by inducing a strong  
30 decrease in diversity, fine sedimentation seems to be a major threat to the functional and ecological integrity  
31 of gravel bars. Overall, these results highlight the conservation priority of low-lying gravel surfaces and the  
32 need to promote more morphologically complex riparian habitats by renaturalizing flow variability and  
33 sediment regimes.

34

35 **1. INTRODUCTION**

36 River ecosystems are intrinsically dynamic and exhibit strong environmental gradients that shape the structure  
37 of communities over space and time (Allan and Castillo, 2007). In free-flowing, i.e., unregulated and  
38 unchannelled rivers, complex hydro-geomorphic processes promote water and sediment exchanges in several  
39 dimensions of the hydrosystem (Ward, 1989). These exchanges allow the creation and renewal of a mosaic of  
40 complex habitats (Junk et al., 1989) that benefit a large number of species (Dudgeon et al., 2006). This is  
41 particularly the case in riparian zones, i.e., in the transitional area between terrestrial and aquatic habitats,  
42 where plant communities face wide variations in disturbance and stress intensities along the flood gradient  
43 (Naiman and Decamps, 1997). These rapid changes in environmental conditions induce a strong turnover in  
44 plant strategies, i.e., from ruderal-anoxia-tolerant species at the bottom of riverbanks to competitive-  
45 desiccation-tolerant species at the top of riverbanks (Janssen et al., 2020a; Kyle and Leishman, 2009; McCoy-  
46 Sulentic et al., 2017). River-floodplain connectivity, conceptualized within the flood pulse framework (Junk et  
47 al., 1989), is thus a key property of hydrosystems capable of ensuring the functionality and ecological integrity  
48 of riparian zones (Naiman and Decamps, 1997).

49 Around the world, river connectivity has been profoundly affected by human infrastructures such as dams and  
50 dikes (Grill et al., 2019; Nilsson et al., 2005). These developments have dramatically altered the flow regime,  
51 i.e., by decreasing the intensity and magnitude of inundations (Poff et al., 2007), as well as the sediment  
52 regime, i.e., by trapping sediment load and favoring fine overbank depositions (Wohl et al., 2015), of most  
53 rivers. These anthropogenic changes have in turn altered the structure and dynamic of riparian communities,  
54 by reducing native species diversity and increasing invasion by exotic species (Catford et al., 2011; Richardson  
55 et al., 2007). Specifically, modifications to the flow and sediment regimes due to regulation/channelization  
56 works has promoted greater uniformity of environmental conditions along local gradients (Poff et al., 2007)  
57 and has lead to a simplification of riparian communities (Aguiar et al., 2018; Bejarano et al., 2018; Tonkin et al.,  
58 2018). This can compromise the ability of degraded rivers to support functional and diverse communities and,  
59 as a result, the wide range of ecosystem services that riparian vegetation delivers to societies (Riis et al., 2020).  
60 Although many studies have documented the impacts of anthropogenic environmental changes on riparian  
61 vegetation, many have focused on woody species and forested habitats established on riverbanks (Aguiar et al.,  
62 2018; Bejarano et al., 2018; Janssen et al., 2020b; Johnson et al., 2012). In regulated and channelized rivers,

63 knowledge of the factors that structure herbaceous communities at fine spatial and temporal scales is thus still  
64 scarce (Su et al., 2020), particularly for riparian habitats of high conservation value, such as gravel bars (Gilvear  
65 et al., 2008). Composed of accumulations of alluvial sediments, these dynamic and morphologically complex  
66 habitats are nevertheless a key element of the river landscape and shelter numerous threatened plant and  
67 animal species (Kalníková et al., 2018; Rottenborn et al., 2018; Zeng et al., 2015). However, due to  
68 anthropogenic changes in flow and sediment regimes, the area of these habitats has been reduced to the  
69 extent that unvegetated or sparsely vegetated bars with mobile sediments are classified as vulnerable in the  
70 European Red List of Habitats (Janssen et al., 2016). To preserve and restore these species-rich riparian habitats  
71 along regulated rivers, it is therefore urgent to better understand the factors that control the structure and  
72 dynamics of herbaceous plant communities on gravel bars over space, i.e., by contrasting the effects of local  
73 and regional gradients at different scales, and time, i.e., by resampling vegetation over several years.

74 In riparian ecology, several recent studies have mobilized a functional trait-based approach to understand the  
75 effects of hydraulic alterations on vegetation (Aguar et al., 2018; Bejarano et al., 2018; Janssen et al., 2020b;  
76 Su et al., 2020; Tabacchi et al., 2019). Combined with a taxonomic approach, this allows us to focus both on  
77 conservation issues, by studying variations in species richness and composition, but also to overcome the limits  
78 of taxonomic studies, under the control of the local species pool, by studying the underlying ecological  
79 mechanisms captured by functional traits (Lavorel et al., 2008). Building on these conceptual foundations, we  
80 used a replicated sampling design spaced two years apart to study the structure and dynamic of plant  
81 communities on gravel bars, at the corridor and site scales, along the highly degraded Rhône River. As shifts in  
82 assemblage patterns are likely to result from a combination of different environmental factors related to the  
83 flow or sediment regimes (e.g., Gilvear et al., 2008; Škornik et al., 2017), we tested the relative influence of a  
84 set of topographic, pedological and hydrological variables on riparian plants, at the community scale.

85 Topographic variables were used to assess the influence of the shape of the bar and thus better guide bank  
86 reprofiling operations. Pedological variables were used to assess the influence of fine sediment deposition and  
87 thus the need to develop specific management plans. Hydrological variables were used to assess the influence  
88 of temporal variations in flows and thus the potential for managing riparian vegetation through environmental  
89 flows. Based on this scheme, we addressed the following two questions: (a) In regulated and channelized  
90 rivers, how and to what extent do environmental conditions and taxonomic and functional  
91 diversity/composition of gravel bar plants vary over a two-year period at the corridor and gravel bar scales? (b)

92 At the community scale, what is the relative influence of topographic, pedological and hydrological variables in  
93 explaining variations in taxonomic and functional diversity/composition over time and space?

94

## 95 **2. MATERIALS & METHODS**

### 96 **2.1. Study area and experimental design**

97 The study was carried out along the Rhône River (total length = 810 km, catchment area = 96,500 km<sup>2</sup>, mean  
98 annual discharge = 1,700 m<sup>3</sup>/s) on a 250 km long stretch of its middle reach (Figure 1). This area is  
99 characterized by a temperate climate with mean annual temperatures and precipitation of 13.6°C and 755 mm  
100 in its southern part and 11.6°C and 815 mm in its northern part. Two historical development phases have  
101 greatly altered the functioning of this river: (i) during the 19<sup>th</sup> century, a correction phase was carried out to  
102 facilitate navigation; (ii) in the second half of the 20<sup>th</sup> century, a derivation phase was carried out to produce  
103 hydropower and facilitate irrigation and navigation (for details see, Bravard and Gaydou, 2015). These two  
104 development phases induced significant impacts in the bypassed reaches (i.e., part of the historical Rhône River  
105 channel), including a channel dewatering due to flow by-passing, reduction in the frequency and magnitude of  
106 the peak flows (Vázquez-Tarrío et al., 2019), and channel stabilization due to engineering infrastructures. These  
107 reaches also underwent a bedload supply interruption due to sediment trapping and extractions at tributary  
108 confluences inducing bed armouring within the main channel. Thus, with the exception of the Miribel bypassed  
109 reach, which is located in the northernmost part of the study area, present-day bedload transport is limited to  
110 fine-grained sediments (Vázquez-Tarrío et al., 2019).

111 During the summer of 2017, we sampled 8 gravel bars (GB1-8) belonging to 7 bypassed reaches, along a north-  
112 south section of about 250 km (Figure 1). The same 8 gravel bars were resampled, at the same location during  
113 the summer of 2019. The studied gravel bars are fixed in the bypassed reaches, i.e., coarse sediments are no  
114 longer remobilized during flood events and are subject to fine-grained overbank sedimentation and  
115 colonization by trees. These large fixed bars correspond to a part of the river bottom before derivation and  
116 represent the only terrestrial habitats available for species within the Rhône riverbed. They are colonized by  
117 different plant communities, dominated by hygrophilic perennial (e.g., *Carex acutiformis*, *Lysimachia vulgaris*,  
118 *Phalaris arundinacea*) or annual species (e.g., *Persicaria lapathifolia*, *Persicaria mitis*, *Rorippa sylvestris*) near  
119 the water line and xero-nitrophilous species (e.g., *Chenopodium album*, *Bromus sterilis*, *Elymus pungens*) at

120 higher elevations. Many exotic species (e.g., *Ambrosia artemisiifolia*, *Aster x salignus*, *Cyperus eragrostis*) have  
121 also taken advantage of these surfaces, forming locally dense patches.

122 To prevent encroachment of gravel bars by woody species and the associated channel narrowing, river  
123 managers periodically rejuvenate the vegetation from the waterline to the edge of the alluvial forest, resulting  
124 in a blockage of plant ecological successions. Specifically, in the study area, the four northern gravel bars (i.e.,  
125 GB1, GB2, GB3 and GB4) are managed by vegetation clearing using a tractor-drawn grinder, while the four  
126 southern gravel bars (i.e., GB5, GB6, GB7 and GB8) are managed by plowing using a bulldozer. These vegetation  
127 maintenance works were performed in the fall, annually for brush clearing and every two years for plowing (in  
128 2016 and 2018 for the southern banks studied).

## 129 **2.2. Vegetation data**

130 On each gravel bar, the vegetation was surveyed along three transects positioned perpendicular to the river in  
131 areas with clear elevation gradients relative to the water surface. The gradients started at the water line and  
132 ended before the alluvial floodplain. Along each transect, four 5 x 5 m quadrats (25 m<sup>2</sup>) were positioned in  
133 homogenous areas while avoiding the aquatic parts of the river margin (i.e., 12 quadrats per gravel bar). Within  
134 each quadrat ( $n_{2017} = 96$ ,  $n_{2019} = 96$ ), all vascular plants were surveyed following the Braun-Blanquet  
135 abundance/dominance methodology (Braun-Blanquet, 1932). Because maintenance works rejuvenated the  
136 bars every year or two, tree and shrub layers were absent and vegetation surveys were conducted by  
137 considering the herbaceous layer only. To account for the time lag in vegetation development between high  
138 and low level quadrat along the topographic gradient, two complete surveys were conducted per year (end of  
139 June and end of July). Then, to characterize the plant community at the scale of each quadrat, the two surveys  
140 were combined by listing all species encountered at least once during the two inventories and associating them  
141 with the highest Braun-Blanquet abundance/dominance coefficient noted. Finally, to limit observer biases, all  
142 surveys were performed by the first author (PJ).

## 143 **2.3. Functional trait data**

144 Three morphological traits – specific leaf area (SLA; leaf area per dry mass), plant height at maturity and seed  
145 mass – were extracted from the TRY database (Kattge et al., 2011). Within Westoby's plant ecology strategy  
146 scheme (Westoby, 1998), these three easily measurable traits, represent three axes of functional trade-offs to  
147 explain plant distribution. SLA is related to resource acquisition and conservation, contrasting “conservative”  
148 species with long-lived leaves to “acquisitive” species with rapid turnover of plant leaves. Plant height at

149 maturity is related to competitive ability, contrasting taller dominant-species with a high ability to pre-empt  
150 resources but with high construction and maintenance costs to smaller dominated-species but with low  
151 construction and maintenance costs. Seed mass is related to dispersal ability, contrasting light-seeded species  
152 but with high seedling mortality to large-seeded species but with high long-term seedling survival.  
153 For each trait, we calculated a mean value per species after removing all trait values with an error risk  $> 3$ , i.e.,  
154 having a maximum distance of 3 standard deviations from at least one of the mean trait values, and applied a  
155  $\log_{10}$ -transformation to comply with normality and to limit extreme values. Then, within each quadrat, we  
156 computed (i) the community-weighted means (CWMs) and (ii) the functional dispersion (FDis) for each of the  
157 three traits (FD package, Laliberté et al., 2014). CWM is defined as the mean of the trait values weighted by the  
158 relative cover of each species bearing each value (Lavorel et al., 2008) and was used as a measure of functional  
159 composition. FDis is defined as the mean distance of individual species to the weighted centroid of all species  
160 in the assemblage (Laliberté and Legendre, 2010) and was used as a measure of functional diversity. Since the  
161 trees/shrubs were present only at the seedling stage and the height values of these species strongly influenced  
162 the calculation of CWM for this trait, we arbitrarily set a height value of 0.10 m for all phanerophyte species ( $n$   
163 = 18, see Appendix S1 for details).  
164 In addition, we studied the response of annual species, i.e., therophytes based on plant life-forms (Raunkiaer,  
165 1934) extracted from the Baseflor database (Julve, 1998), which constitute communities often with high  
166 conservation stakes on gravel bars (e.g., Rottenborn et al., 2018), and exotic species, based on a regional  
167 hierarchical list of invasive species (Debay et al., 2020), which represent potential threats to native species  
168 (Richardson et al., 2007) (see detailed information for each species in Appendix S1).

#### 169 **2.4. Environmental variables**

170 At the center of each quadrat, the elevation difference and distance to the water line were characterized using  
171 topographical surveys. Topographic measurements were conducted using a laser rangefinder (TruPulse 200X)  
172 positioned on a tripod at a constant height of 1.2 m and a target at a height of 2.0 m. The horizontal and  
173 vertical distances between the tripod and the target were measured between the water line at the beginning  
174 of each transect and the center of the four successive quadrats. For soil properties, the proportion of subsoil  
175 fine sediment was derived from two soil core samples (30-cm thickness) collected in representative areas  
176 within each quadrat and pooled together. Each composite soil sample was then dried, weighed and sieved in  
177 the laboratory to estimate the proportion of fine sediments (i.e.,  $<250\text{-}\mu\text{m}$  mesh). Moreover, fine sediment



178 thickness was estimated at the center of each quadrat using a soil corer inserted into the sediment up to the  
179 interface with the gravel, and measuring the distance from the surface. All of these measurements were made  
180 on each gravel bar in 2017 and 2019 during the survey carried out in June (for illustration of the variations in  
181 topographic and pedological variables, within and between gravel bars, see Appendix S2).

182 For hydrological variables, the water elevation (m) of the Rhône was calculated for each transect using a 1D  
183 hydrodynamic model based on the 1D shallow water equations (for details, see Dugué et al., 2015; Launay et  
184 al., 2019). This numerical model covers the entire length of the French Rhône, including its main tributaries and  
185 operation rules of hydropower structures. It has been calibrated and validated on each reach using longitudinal  
186 water profiles, provided by the Compagnie Nationale du Rhône, over a wide range of discharges for frequent  
187 hydrological events. The model correctly reproduces discharge time-series, especially during floods. For low  
188 flow periods, results are not as accurate due to hydropower scheme subdaily operations that are not included  
189 in the model. The output of the model provides a detailed elevation of the water, due to the real geometry of  
190 the river bed as a series of cross-sections every 200-500 meters and the high temporal resolution of the hourly  
191 results at any point in the model. Combined with centimetric measures of the quadrat elevation, we were able  
192 to calculate two hydrological variables: the inundation duration, i.e., the sum of hourly measurements below  
193 the water level expressed in days, and the inundation intensity, i.e., the highest water level expressed in  
194 meters. For each quadrat, these variables were calculated considering a time extension from September 1 to  
195 August 31 for the 2016/2017 and 2018/2019 periods (Appendix S3).

## 196 **2.6. Statistical analysis**

197 The continuous independent variables were the elevation difference (denoted "Elevation" in tables and figures)  
198 and distance to water line ("Distance"), the proportion ("Prop\_Sedim") and thickness ("Thick\_Sedim") of fine  
199 sediments, the duration ("Dura\_Inund") and intensity ("Inte\_Inund") of inundation (Appendix S4). The  
200 independent factors were the year of sampling ("Year", two-level factor), the gravel bar ("GB", eight-level  
201 factor) and maintenance measures ("Manag", two-level factor). The skewed variables "Thick\_Sedim" and  
202 "Dura\_Inund" were  $\log_{10}$ -transformed while the "Prop\_Sedim" (i.e., proportional data) was logit transformed.  
203 Finally, all continuous variables were standardized before performing the analyses.

204 To determine whether environmental conditions, taxonomic diversity, i.e., the richness of total, annual and  
205 exotic species, and functional diversity, i.e., the functional dispersion (i.e., FDis) of SLA, height and seed trait  
206 values, varied between 2017 and 2019, between gravel bars managed by brush clearing or plowing, as well as

207 with the interaction between both factors, we used two-way ANOVAs (stats package). To determine whether  
208 environmental conditions, taxonomic diversity and functional diversity varied over time within each bar we  
209 used paired *t*-test (stats package). We also used paired *t*-test to determine how inundation duration and  
210 intensity varied along the elevation gradient, i.e. in each quadrat position, between years. As multiple  
211 comparison tests were performed, we adjusted the p-values with the Benjamini and Hochberg correction.  
212 To determine how environmental conditions explained differences in taxonomic and functional diversity  
213 between years, at the community scale, we used a modeling approach. We considered a set of 12 *a priori*  
214 models, testing additive and interactive effects between the six environmental variables and year, plus a null  
215 model (Appendix S5). Since observations within each bar were not independent, we used mixed models with  
216 “GB” as a random effect (lme4 package, Bates et al., 2015). Also, because maintenance measures influenced  
217 significantly the taxonomic diversity, we included “Manag” as a covariate in all *a priori* models. We then fitted  
218 mixed models with a Poisson distribution to study variations in species richness and with a Normal distribution  
219 to study variations in trait dispersion. To identify the most parsimonious model, we used Akaike’s information  
220 criterion corrected for small sample sizes and performed model averaging, based on all *a priori* models, to  
221 estimate the parameters and associated unconditional standard errors (MuMIn package, Barton, 2015).  
222 To determine whether the taxonomic composition and functional composition varied between 2017 and 2019,  
223 between gravel bars managed by brush clearing or plowing, as well as with the interaction between both  
224 factors, we used two-way PERMANOVAs (Anderson and Walsh, 2013) with 999 permutations (vegan package,  
225 Oksanen et al., 2013). For the taxonomic composition, we used a Hellinger distance matrix based on the cover  
226 of each species in each of the quadrats, while for the functional composition, we used a Euclidean distance  
227 matrix based on the mean values of each trait (i.e., CWM) in each of the quadrats. As multiple comparison tests  
228 were performed, we adjusted the p-values with the Benjamini and Hochberg correction. To determine whether  
229 the taxonomic composition and functional composition varied over time within each bar we used one-way  
230 PERMANOVAs and adjusted the p-values with the Benjamini and Hochberg correction.  
231 To determine how variations in environmental conditions explained differences in taxonomic and functional  
232 composition, at the community scale, we used canonical analysis of principal coordinates (CAP, Anderson and  
233 Willis, 2003), with 999 permutations (vegan package, Oksanen et al., 2013). We then calculated the marginal  
234 contribution of all independent variables to total constrained inertia and tested for their individual significance  
235 (after all other variables were partialled out).

236 Analyses were performed with R version 3.5.1 (R Core Team, 2020) (see a summary of the statistical analyses  
237 performed in Appendix S6).

238

### 239 **3. RESULTS**

#### 240 **3.1. Changes in environmental conditions between years**

241 Two-way ANOVAs showed that, on average, inundation intensity within quadrats was significantly lower in  
242 2019 than in 2017, and that this effect was more pronounced on gravel bars managed by plowing, i.e. a  
243 significant interaction effect (Table 1). In addition, compared to quadrats located on gravel bars managed by  
244 brush clearing, quadrats on bars managed by plowing were at a shorter average distance and higher average  
245 elevation from the water line. In the same quadrats, i.e. managed by plowing, the average thickness of fine  
246 sediments, as well as the average duration of inundation, were significantly lower.

247 Paired *t*-test showed that within gravel bars, the elevation increased significantly between 2017 and 2019 on  
248 GB3 but decreased on GB7 and GB8, while the distance to water increased on GB5 but decreased on GB8. The  
249 proportion of fine sediments increased significantly between years on GB2, GB4 and GB8 but decreased on  
250 GB3, while the thickness of fine sediments decreased only on GB7. Finally, inundation intensity decreased  
251 significantly between years on all bars, except on GB1 where it increased, while inundation duration increased  
252 on GB1 and GB8 but decreased on GB3, GB5, GB6 and GB7 (Figure 2 & detailed results in Appendix S7).

253 However, while inundations were more intense in 2017 regardless of quadrat position along the elevation  
254 gradient, they were longer in 2019 on low-level quadrats composed of coarse-grained sediments (Appendix  
255 S8).

#### 256 **3.2. Changes in taxonomic and functional diversity between years**

257 A total of 205 species (mean  $\pm$ SD = 21  $\pm$ 12) were recorded in the 192 quadrats along the Rhône River. Among  
258 these, 38 were exotic and 87 were annual.

259 Two-way ANOVAs showed that, on average, the richness of total, annual and exotic species within the quadrats  
260 decreased significantly between 2017 and 2019, while for functional diversity, trait dispersion values (i.e., FDis)  
261 remained stable (Table 1). In addition, the average richness of total, annual and exotic species, as well as the  
262 functional dispersion values of seed mass within the quadrats decreased significantly on gravel bars managed  
263 by brush clearing as compared to gravel bars managed by plowing. However, none of the measures of

264 taxonomic and functional diversity was significantly influenced by the interaction between the years and  
265 management factors.

266 Paired *t*-test showed that within gravel bars, species richness decreased significantly between 2017 and 2019  
267 on GB1, GB2, GB6 and GB8; functional dispersion values for plant height, seed mass and specific leaf area  
268 decreased significantly between years on GB2; functional dispersion value for plant height increased  
269 significantly between years on GB8 (Figure 3 & detailed results in Appendix S9).

### 270 **3.3. Changes in taxonomic and functional diversity with environmental conditions**

271 Mixed models showed that models including pedological variables ranked first for the richness of annual and  
272 exotic species and the functional dispersion values (i.e., FDis) of height and seed mass values, while models  
273 including hydrological variables ranked first for total richness and the functional dispersion value of SLA (Table  
274 2 & detailed results in Appendix S10). Model averaging revealed that total, annual and exotic species richness,  
275 as well as the functional dispersion value of seed mass were higher on bars maintained by plowing than on bars  
276 maintained by brush clearing (Table 3). Also, the proportion and thickness of fine sediments had a significant  
277 negative effect on species richness and the functional dispersion values of SLA and height. However, for species  
278 richness, the interaction between fine sediments proportion and years was significant, revealing a large  
279 variation in richness over time on the surfaces made up of coarse-grained sediments (see interaction plots in  
280 Appendix S11). Total and exotic species richness, as well as the functional dispersion value of SLA, also  
281 decreased with increasing elevation, while all richness measures varied more between years on the surfaces  
282 closest to water. Conversely, total species richness and the functional dispersion value of SLA increased on  
283 more intensely inundated surfaces, while all richness measures as well as the functional dispersion value of SLA  
284 increased with inundation duration in 2017 but decreased in 2019.

### 285 **3.4. Changes in taxonomic and functional composition between years**

286 Two-way PERMANOVAs showed that the taxonomic composition differed significantly between 2017 and 2019  
287 ( $F_{1,188} = 2.880, p = 0.002$ ), while the functional composition (i.e., CWM) did not ( $F_{1,188} = 1.201, p = 0.297$ ) (Figure  
288 4). In addition, the taxonomic composition differed significantly between gravel bars managed by brush  
289 clearing and gravel bars managed by plowing ( $F_{1,188} = 15.395, p = 0.001$ ), while the functional composition did  
290 not ( $F_{1,188} = 2.573, p = 0.106$ ). However, both the taxonomic ( $F_{1,188} = 1.348, p = 0.130$ ) and the functional ( $F_{1,188} =$   
291  $1.016, p = 0.343$ ) composition were not significantly influenced by the interaction between the years and  
292 management factors.

293 Within gravel bars, one-way PERMANOVAS showed that the taxonomic composition changed between 2017  
294 and 2019 on GB7 ( $F_{1,22} = 5.032$ ,  $p$ -adjust = 0.004) and GB8 ( $F_{1,22} = 5.027$ ,  $p$ -adjust = 0.004), while the functional  
295 composition changed only on GB7 ( $F_{1,22} = 17.789$ ,  $p$ -adjust = 0.016).

### 296 **3.5. Changes in taxonomic and functional composition with environmental conditions**

297 Canonical analysis of principal coordinates showed that 16.8% ( $F_{6,185} = 7.415$ ,  $p = 0.001$ ) of the variation in  
298 taxonomic composition and 22.9% ( $F_{6,185} = 10.475$ ,  $p = 0.001$ ) of the variation in functional composition were  
299 explained by environmental variables (Figure 5). For the taxonomic composition, the first CAP axis was  
300 positively related to elevation level and distance to water, which respectively explained 33.6% ( $p = 0.001$ ) and  
301 10.1% ( $p = 0.001$ ) of the constrained inertia, and negatively related to the duration (8.4%,  $p = 0.001$ ) and  
302 intensity (12.2%,  $p = 0.001$ ) of inundations. The second CAP axis was negatively related to the proportion  
303 (20.6%,  $p = 0.001$ ) and thickness (14.9%,  $p = 0.001$ ) of fine sediments. For the functional composition, the first  
304 CAP axis was positively related to elevation level (26.8%,  $p = 0.001$ ) and distance to water (2.2%,  $p = 0.001$ ), but  
305 negatively to the duration (6.0%,  $p = 0.001$ ) and intensity (1.7%,  $p = 0.008$ ) of inundations. The second CAP axis  
306 was positively related to the proportion (22.6%,  $p = 0.001$ ) and thickness (40.7%,  $p = 0.001$ ) of fine sediments.

307

## 308 **4. DISCUSSION**

309 Understanding the interactions between fluvial landforms and vegetation dynamics is essential for success in  
310 restoring biodiversity and functionality to riparian communities on corridors heavily modified by human  
311 activities (Palmer and Ruhi, 2019). By studying variations of abiotic and biotic conditions at the corridor and  
312 gravel bar scales along the highly modified Rhône River between two seasons in 2017 and 2019, we showed  
313 that (i) environmental conditions varied a little from year to year; (ii) taxonomic measures clearly tracked  
314 environmental changes; (iii) functional measures were stable over time. Specifically, we showed that variations  
315 in richness and composition of herbaceous plants between the two years and sites were largely limited to  
316 species sharing the same trait values, underscoring the functional resilience of riparian communities to  
317 environmental changes. Also, we highlighted that the strongest variations in taxonomic diversity between the  
318 years 2017 and 2019 were spatially restricted to low elevation surfaces, made up of coarse-grained sediments  
319 and more frequently flooded. Beyond being the most vulnerable, riparian communities established under these  
320 conditions were also the most taxonomically and functionally diverse. To improve both the biodiversity and

321 functionality of riparian herbaceous communities along the Rhône River, the conservation and restorations of  
322 these gravel bar habitats should be a priority.

#### 323 **4.1. River regulation and bank stabilization lead to relatively stable riparian habitats**

324 At the corridor scale there was no variation in topographic and pedological conditions between the two years.  
325 Within the gravel bars, changes of low magnitudes were found between 2017 and 2019, mostly limited to  
326 variations in the proportion of fine sediments. Although it cannot be ruled out that these small variations are  
327 the results of methodological biases in the field measurements, this tends to confirm that hydro-geomorphic  
328 processes along the Rhône River are limited to fine-grained sediments (Tena et al., 2020; Vauclin et al., 2020).  
329 Conversely, even if 2017 and 2019 were “calm” hydrological years, i.e., none of the peak flows recorded  
330 exceeded the two-year return flood of the Rhône, at the corridor scale, a significant decrease in the intensity of  
331 inundation could still be measured between the two years. Within the gravel bars and with the exception of  
332 GB1, our results confirmed that inundations were more intense in 2017 but that their duration were either  
333 longer or shorter depending on the site. However, additional analyses of floods duration showed  
334 heterogeneous variations along the elevation gradient and with the extent of fine sediment deposits (Appendix  
335 S8). Thus, while mid- and high-level quadrats were inundated on average one day longer in 2017, low-level  
336 quadrats, especially if they were composed of coarse-grained sediments, were inundated up to 20 days longer  
337 in 2019. This shows that in this regulated and channelized river system, where the bypassed reaches receive  
338 only a minimum baseflow (i.e., the residual flow is 10-30% of the mean annual flow arriving at the upstream  
339 diversion dams) and are subject to a sharp reduction in the frequency and magnitude of peak flows (Vázquez-  
340 Tarrío et al., 2019), environmental factors indirectly related to the characteristics of the gravel bars are the  
341 main sources of variation that can shape riparian communities. Moreover, this tends to confirm that water and  
342 sediment exchanges, as well as scouring, in the absence of important floods, as was the case during this short  
343 study period, are very limited in the bypassed reaches (Vázquez-Tarrío et al., 2019) and do not allow, under  
344 current hydrological conditions, the creation or renewal of riparian habitats in the Rhône riverbed.

#### 345 **4.2. Taxonomic diversity and composition respond to environmental changes in space and time**

346 Species richness decreased between 2017 and 2019 at the corridor scale and followed a similar trend within  
347 each of the bar. Specifically, we showed that maintenance measures, which are confused with the longitudinal  
348 and climatic gradient, strongly influenced richness, i.e., northern bars maintained by brush clearing were  
349 species poor than southern bars maintained by plowing. By disturbing the soil surface, plowing artificially

350 increases microtopographic variations on bars (*sensu*, Pollock et al., 1998), allowing greater local co-occurrence  
351 of species with contrasting habitat requirements (Janssen et al., 2019). After controlling for this confounding  
352 spatial effect, which was constant between the two years studied, we demonstrated that temporal changes in  
353 richness were independent of management practices and involved communities established under specific  
354 environmental conditions. Indeed, plant richness varied more between years at low elevations, on more  
355 frequently flooded surfaces consisting of coarse-grained sediments. Since flooding on the Rhone was shown to  
356 be more intense in 2017 regardless of quadrat position along the elevation gradient, but longer in 2019 at the  
357 low-level quadrats composed of coarse-grained sediments, we infer that these variations in hydrological  
358 conditions were the primary cause of species loss. Indeed, it was shown that flooded areas received a more  
359 diverse pool of colonizing species through hydrochory (Gurnell et al., 2008; Jansson et al., 2005) but also that  
360 intermediate-intensity floods supported high species diversity (Pollock et al., 1998; Renofalt et al., 2005).  
361 However, over the two years studied, the magnitude of flooding varied within a narrow range, and the peak  
362 flows recorded cannot be characterized as intermediate disturbances (Appendix S3). At the same time, it has  
363 been shown that frequently flooded sites with low spatial variation in flood frequencies are species-poor  
364 (Pollock et al., 1998) but also that in dam-regulated rivers, long unnatural inundations have a negatively effect  
365 on species richness (e.g., Su et al., 2020; Zheng et al., 2021). On the Rhone, the spatial structuring of  
366 inundations, longer in 2019 at low levels on pebble-dominated bars, and of species richness, lower in 2019 in  
367 low-lying quadrats composed of coarse-grained sediments, supports these previous finding. Specifically, our  
368 results suggest that a prolonged submergence of about 20 days can induce a strong decrease in the taxonomic  
369 diversity of riparian herbaceous communities and highlight, in this highly regulated river system, the greater  
370 vulnerability of plant species established on bar surfaces made up of coarse-grained sediments to variations in  
371 hydrological conditions. Since along the gravel bars of the Rhone, as in other rivers (Kalníková et al., 2018;  
372 Škornik et al., 2017), species richness is highest in these riparian habitats, we believe that their conservation  
373 should be a priority (Gilvear et al., 2008; Rottenborn et al., 2018; Zeng et al., 2015).

374 Species composition also varied between the two years studied at the corridor scale. Within bars, changes in  
375 composition between years were however restricted to only two sites, which may be due to the small temporal  
376 extent of this study but also to management practices that periodically reset succession. Furthermore,  
377 community-wide analyses revealed that compositional changes were primarily explained by bar characteristics.  
378 Indeed, elevation difference explained most of the variation (Gilvear et al., 2008; Kalníková et al., 2018; Škornik

379 et al., 2017), with a shift from flood-tolerant species at low elevation (e.g., *Phalaris arundinacea* and  
380 *Phragmites australis*) to drought-tolerant species at high elevation (e.g., *Lolium perenne* and *Elymus repens*).  
381 Also, the proportion of fine sediments on the bars profoundly influenced species composition (Gilvear et al.,  
382 2008; Kalníková et al., 2018). Thus, at low elevation, *Phalaris arundinacea* cover increased when there was little  
383 fine sediment while *Phragmites australis* cover increased when there was a lot of fine sediment, and, at high  
384 elevation, *Lolium perenne* cover increased when there was little fine sediment while *Elymus repens* cover  
385 increased when there was a lot of fine sediment. Beyond bar characteristics, hydrological conditions  
386 during the year preceding observations were of little inference value to explain changes in herbaceous plant  
387 composition in our study system. This is likely related to the fact that the Rhone floods were of too low  
388 intensity in 2017 and 2019 to trigger the scouring process necessary to initiate a new succession (Steiger et al.,  
389 2005). Overall, these results show that, even in a regulated river system, the taxonomic composition of riparian  
390 habitats remained under the influence of multiple environmental gradients, acting at both the local and  
391 regional scales (Kuglerová et al., 2015; Renofalt et al., 2005).

#### 392 **4.3. Traits diversity and functional composition remain stable in space and time**

393 In contrast to species richness, functional dispersion values remained stable over time at the corridor and  
394 gravel bar scales, with the exception of GB2. This suggests that the herbaceous species that disappeared  
395 between 2017 and 2019 on the Rhone gravel bars had redundant trait values in the community, showing some  
396 functional resilience of this regulated system to environmental changes (Su et al., 2020). Also, trait dispersion  
397 for specific leaf area (SLA) was higher on GB1, which is located in the only bypassed reach where bedload  
398 transport is still active (Vázquez-Tarrío et al., 2019). Greater co-occurrence of species with different resource  
399 acquisition and conservation strategies on "active" bars may confirm that flood disturbance increases  
400 functional diversity (Biswas and Mallik, 2010; Lawson et al., 2015) and suggests the use of leaf traits as  
401 potential indicators of riparian habitat dynamics. Conversely, the functional dispersion value for seed mass was  
402 strictly influenced by maintenance measures. Indeed, plowing by increasing microtopographic heterogeneity,  
403 allows a variation in flood frequencies and velocity conditions (Pollock et al., 1998), thus the deposition of light  
404 and heavy seeds on restricted surfaces. Controlling for this spatial effect, community-wide analyses confirmed  
405 that trait dispersion was nearly unaffected by changes in environmental conditions between the two years  
406 studied. However, functional diversity peaked under the same environmental conditions as taxonomic  
407 diversity. Specifically, we showed that bars covered by a thick layer of fine sediments supported species with a



408 narrow range of trait values (see also, Janssen et al., 2019). Thus, even for fixed bars in a highly regulated river  
409 system, as is the case of the Rhône, the co-occurrence of herbaceous species with different functional  
410 strategies was greater when they consisted of coarse sediments (Janssen et al., 2020a). This is particularly true  
411 at low elevations, on surfaces more intensely flooded (Lawson et al., 2015).

412 Functional composition did not vary between years at the corridor scale. Within bars, changes in trait  
413 composition between 2017 and 2019 was restricted to one site. This confirms the stability of functional  
414 assemblages in space and time, probably due to the low amplitude of hydrological conditions over the two  
415 years studied on the Rhone River, and emphasizes that changes in species identity between gravel bars along  
416 the Rhône River do not result in changes in trait values. Regarding the influence of environmental conditions,  
417 soil factors explained up to 60% of the variation in the functional composition of riparian herbaceous  
418 communities. Specifically, we showed that accumulation of fine sediment on gravel bars resulted in an increase  
419 in mean plant height (Kyle and Leishman, 2009). Indeed, silt deposits, by promoting fertile environments  
420 (Asaeda and Rashid, 2012), favoured the development of taller dominant-species capable of pre-empting  
421 resources, such as *Phragmites australis* (Minchinton and Bertness, 2003) and *Phalaris arundinacea* (Chen et al.,  
422 2017). Moreover, as these taller species are more typical of lentic aquatic ecosystems, the high cover measured  
423 on the bars of the Rhone affected by fine sediment deposits may also reflect their adaptation to the fairly  
424 constant minimum flow that is observed most of the year in the bypassed sections. In addition to soil texture,  
425 elevation level also explained much of the functional composition, with an increase in mean seed mass from  
426 low to high elevation (Kyle and Leishman, 2009; McCoy-Sulentic et al., 2017). This tends to confirm that the  
427 colonization potential of light-seeded species (e.g., *Artemisia annua*, *Juncus articulatus*, *Veronica anagallis-*  
428 *aquatica*) is higher in more frequently disturbed environments (Gurnell et al., 2008), this even in a highly  
429 regulated river system. Beside bar characteristics and certainly due to the low magnitude of inundations in the  
430 months preceding the field observations in 2017 and 2019, hydrological conditions did not explain much of the  
431 functional composition of communities. Overall, we showed that at the corridor scale, high species turnover  
432 along the longitudinal-climatic gradient did not lead to a shift in the functional composition of riparian  
433 communities, whereas at the gravel bar scale, trait-environment relationships varied strongly and consistently  
434 with local gradients in elevation and soil texture. This underlines, at least for highly regulated river systems and  
435 for the range of hydrological conditions studied, the greater relative importance of local processes in  
436 controlling the functioning of riparian communities.

437

438 **5. CONCLUSION**

439 By studying spatial and temporal variations in riparian herbaceous communities along the heavily modified  
440 Rhône River, we showed (1) that different gravel bars supported different species pools, which shared almost  
441 the same set of traits, and (2) that changes in richness over the two-year period were restricted to species with  
442 redundant trait values in the communities, suggesting some functional resilience to environmental changes.  
443 Furthermore, by investigating the relative influence of different environmental factors on assemblage patterns,  
444 we showed that the temporal change in taxonomic diversity was spatially restricted to communities  
445 established on low-lying bar surfaces composed of coarse-grained sediments, which were more intensely and  
446 frequently flooded. In addition to being the most sensitive to environmental changes, the riparian communities  
447 established on these surfaces were also the most diverse in species and trait values, highlighting the  
448 importance of these habitats for the Rhone river biodiversity and functionality. However, in this regulated river  
449 system where water and sediment exchanges are very limited, we showed that fine sediment deposition  
450 threatens the functional and ecological integrity of gravel bars by inducing a strong decrease in species and  
451 trait diversity. Although consistent and supported by other studies on different systems, these results are still  
452 limited to a short observation period and concerns an intensively managed river system, where a lagged  
453 response of the vegetation to environmental changes cannot be excluded. To better disentangle the relative  
454 influence of the many environmental parameters that condition riparian community dynamics, longer,  
455 replicated observational studies are needed. Finally, from an applied perspective and in order to improve the  
456 biodiversity and functionality of riparian habitats in regulated rivers, our results highlight the urgent  
457 importance of conserving still-functional gravel bars and promoting more morphologically complex riparian  
458 habitats. This could be achieved by developing management plans, at the corridor and reach scales, aiming at  
459 renaturalize the flow regime (e.g., by increasing and irregularizing baseflows, Lawson et al., 2015) and  
460 reactivate bedload supply and transport (e.g., through gravel augmentation, Staentzel et al., 2020) to maximize  
461 scouring and prevent fine sediment deposits. Applied to restoration operations aimed at improving lateral  
462 connectivity through the removals of dykes, our results suggest that it would be more beneficial for biodiversity  
463 to profile banks with a gentle slope and to favor materials with a predominance of coarse-grained sediments.

464

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476

#### 477 **DATA AVAILABILITY STATEMENT**

478 Data are available from the authors upon reasonable request.

479

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675

676 **Table 1.** Variations in environmental conditions, taxonomic and functional diversity between years and maintenance measures, as well as the interaction between both  
 677 factors, along the Rhône River, France ( $F$ -value<sub>(3,188)</sub> and  $p$ -value based on two-way ANOVAs, SD = standard deviation, FDis = Functional Dispersion, SLA = Specific Leaf Area)

Variables	2017 : mean ( $\pm$ SD)		2019 : mean ( $\pm$ SD)		Year		Management		Interaction	
	Clearing	Plowing	Clearing	Plowing	F	$p$ -value	F	$p$ -value	F	$p$ -value
<i>Environmental conditions</i>										
Elevation above water line (m)	1.14 ( $\pm$ 0.78)	1.00 ( $\pm$ 0.72)	1.20 ( $\pm$ 0.87)	0.88 ( $\pm$ 0.74)	0.086	0.770	4.249	0.041	0.667	0.415
Distance to water line (m)	28.43 ( $\pm$ 21.06)	34.92 ( $\pm$ 25.84)	28.56 ( $\pm$ 20.60)	35.54 ( $\pm$ 25.98)	0.012	0.912	3.941	0.049	0.005	0.942
Proportion of fine sediments (%)	43.20 ( $\pm$ 34.73)	37.16 ( $\pm$ 34.79)	39.06 ( $\pm$ 37.61)	32.95 ( $\pm$ 31.24)	0.014	0.906	0.607	0.437	0.185	0.667
Thickness of fine sediments (cm)	22.81 ( $\pm$ 27.11)	18.14 ( $\pm$ 27.35)	28.35 ( $\pm$ 32.56)	18.36 ( $\pm$ 26.86)	0.005	0.946	7.404	0.007	0.254	0.615
Inundation duration (days)	15.20 ( $\pm$ 12.69)	11.48 ( $\pm$ 9.30)	19.26 ( $\pm$ 22.60)	10.20 ( $\pm$ 11.81)	1.400	0.238	9.426	0.002	1.038	0.310
Inundation intensity (m)	2.11 ( $\pm$ 0.89)	2.97 ( $\pm$ 1.81)	1.93 ( $\pm$ 0.94)	1.74 ( $\pm$ 0.92)	16.546	0.000	3.664	0.057	9.106	0.003
<i>Taxonomic diversity</i>										
Total species richness	18.35 ( $\pm$ 9.12)	31.29 ( $\pm$ 11.61)	11.96 ( $\pm$ 4.92)	25.00 ( $\pm$ 10.95)	21.336	0.000	89.456	0.000	0.001	0.970
Richness of annual species	6.19 ( $\pm$ 5.83)	14.92 ( $\pm$ 6.09)	3.69 ( $\pm$ 2.49)	11.71 ( $\pm$ 6.04)	13.758	0.000	118.459	0.000	0.212	0.646
Richness of exotic species	4.21 ( $\pm$ 3.38)	8.94 ( $\pm$ 3.45)	2.67 ( $\pm$ 1.74)	7.54 ( $\pm$ 3.91)	9.956	0.002	106.425	0.000	0.025	0.876
<i>Functional diversity</i>										
FDis of SLA trait values	0.64 ( $\pm$ 0.32)	0.61 ( $\pm$ 0.25)	0.59 ( $\pm$ 0.29)	0.59 ( $\pm$ 0.21)	0.925	0.337	0.242	0.623	0.110	0.741
FDis of plant height trait values	0.70 ( $\pm$ 0.26)	0.62 ( $\pm$ 0.18)	0.64 ( $\pm$ 0.35)	0.64 ( $\pm$ 0.24)	0.125	0.725	1.048	0.307	1.022	0.313

FDis of seed mass trait values	0.56 ( $\pm 0.23$ )	0.70 ( $\pm 0.29$ )	0.50 ( $\pm 0.25$ )	0.72 ( $\pm 0.22$ )	0.355	0.552	26.414	0.000	1.371	0.243
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678

679 **Table 2.** Top three among 13 top-ranking models predicting taxonomic and functional diversity of riparian  
680 plants on gravel bars, at the community scale, along the Rhône River (France), as assessed with the Akaike  
681 information criterion corrected for small sample size (AICc). Number of estimated parameters including the  
682 intercept and random effect (k), AICc value, difference in AICc ( $\Delta$ AICc), AICc weight (*W*) and marginal coefficient  
683 of determination for fixed effect ( $R^2_{\text{marginal}}$ ) are provided (for the description of model parameters, please refer  
684 to Table 1)

Dependent variable	Model (fixed-effects)	k	AICc	$\Delta$ AICc	W	$R^2_{\text{marginal}}$
Total richness	Manag + Year * Dura_Inund	6	1601.5	0.000	0.390	0.651
Total richness	Manag + Year + Elevation	5	1602.1	0.627	0.285	0.658
Total richness	Manag + Year * Thick_Sedim	6	1603.9	2.435	0.115	0.648
Annual richness	Manag + Year * Thick_Sedim	6	1262.3	0.000	0.887	0.710
Annual richness	Manag + Year + Thick_Sedim	5	1266.4	4.148	0.112	0.716
Annual richness	Manag + Year * Prop_Sedim	6	1275.4	13.160	0.001	0.691
Exotic richness	Manag + Year + Thick_Sedim	5	983.1	0.000	0.477	0.555
Exotic richness	Manag + Year * Thick_Sedim	6	983.7	0.621	0.350	0.551
Exotic richness	Manag + Year * Prop_Sedim	6	986.6	3.511	0.082	0.539
FDis SLA	Manag + Year * Dura_Inund	7	16.2	0.000	0.368	0.130
FDis SLA	Manag + Year + Thick_Sedim	6	17.8	1.626	0.163	0.144
FDis SLA	Manag + Year + Prop_Sedim	6	18.2	2.009	0.135	0.142
FDis height	Manag + Year + Prop_Sedim	6	30.3	0.000	0.571	0.061
FDis height	Manag + Year * Prop_Sedim	7	32.2	1.931	0.217	0.062
FDis height	Manag + Year + Thick_Sedim	6	33.1	2.871	0.136	0.047
FDis seed	Manag + Year * Thick_Sedim	7	-8.9	0.000	0.415	0.184
FDis seed	Manag + Year + Thick_Sedim	6	-8.8	0.067	0.401	0.177
FDis seed	Manag + Year + Prop_Sedim	6	-4.8	4.027	0.055	0.156

685

686 **Table 3.** Relative importance (Imp.), estimate coefficients (Estimate ( $\pm$  SE)) and confidence intervals (95% CI) for each variable used to predict variations in taxonomic and  
687 functional diversity of riparian plants on gravel bars along the Rhône River, France. The 95% confidence interval of coefficients in bold excluded 0. For the maintenance  
688 measures (Manag) and year of sampling (Year) factors, positive estimates represent plowing or 2019, while negative estimates represent brush clearing or 2018 (refer to  
689 Table 1 for the description of the other variables)

Parameters	Total richness			Annual richness			Exotic richness		
	Imp.	Estimate ( $\pm$ SE)	(95% CI)	Imp.	Estimate ( $\pm$ SE)	(95% CI)	Imp.	Estimate ( $\pm$ SE)	(95% CI)
Year	<b>1.00</b>	<b>-0.293 (<math>\pm</math>0.033)</b>	<b>(-0.357; -0.229)</b>	<b>1.00</b>	<b>-0.299 (<math>\pm</math>0.051)</b>	<b>(-0.400; -0.199)</b>	<b>1.00</b>	<b>-0.253 (<math>\pm</math>0.062)</b>	<b>(-0.373; -0.132)</b>
Management	<b>1.00</b>	<b>0.599 (<math>\pm</math>0.105)</b>	<b>(0.393; 0.804)</b>	<b>1.00</b>	<b>0.944 (<math>\pm</math>0.149)</b>	<b>(0.652; 1.237)</b>	<b>1.00</b>	<b>0.828 (<math>\pm</math>0.111)</b>	<b>(0.610; 1.046)</b>
Elevation	<b>0.38</b>	<b>-0.078 (<math>\pm</math>0.019)</b>	<b>(-0.115; -0.040)</b>	0.00	-0.007 ( $\pm$ 0.030)	(-0.065; 0.052)	<b>0.03</b>	<b>-0.092 (<math>\pm</math>0.038)</b>	<b>(-0.166; -0.018)</b>
Distance	<b>0.00</b>	<b>-0.070 (<math>\pm</math>0.022)</b>	<b>(-0.112; -0.027)</b>	0.00	-0.033 ( $\pm$ 0.034)	(-0.100; 0.033)	0.00	-0.062 ( $\pm$ 0.044)	(-0.148; 0.024)
Prop_Sedim	<b>0.03</b>	<b>-0.106 (<math>\pm</math>0.028)</b>	<b>(-0.161; -0.050)</b>	<b>0.00</b>	<b>-0.280 (<math>\pm</math>0.045)</b>	<b>(-0.368; -0.193)</b>	<b>0.09</b>	<b>-0.163 (<math>\pm</math>0.055)</b>	<b>(-0.271; -0.055)</b>
Thick_Sedim	<b>0.20</b>	<b>-0.111 (<math>\pm</math>0.029)</b>	<b>(-0.168; -0.054)</b>	<b>1.00</b>	<b>-0.307 (<math>\pm</math>0.047)</b>	<b>(-0.400; -0.215)</b>	<b>0.83</b>	<b>-0.162 (<math>\pm</math>0.049)</b>	<b>(-0.259; -0.066)</b>
Dura_Inund	<b>0.39</b>	<b>0.132 (<math>\pm</math>0.029)</b>	<b>(0.076; 0.189)</b>	0.00	0.032 ( $\pm$ 0.045)	(-0.056; 0.121)	<b>0.05</b>	<b>0.156 (<math>\pm</math>0.057)</b>	<b>(0.045; 0.267)</b>
Inte_Inund	<b>0.00</b>	<b>0.061 (<math>\pm</math>0.025)</b>	<b>(0.012; 0.111)</b>	<b>0.00</b>	<b>0.094 (<math>\pm</math>0.037)</b>	<b>(0.022; 0.166)</b>	0.00	0.056 ( $\pm$ 0.044)	(-0.030; 0.142)
Year * Elevation	0.10	0.003 ( $\pm$ 0.033)	(-0.061; 0.068)	0.00	-0.023 ( $\pm$ 0.051)	(-0.122; 0.076)	0.01	0.026 ( $\pm$ 0.065)	(-0.101; 0.154)
Year * Distance	<b>0.00</b>	<b>0.085 (<math>\pm</math>0.030)</b>	<b>(0.026; 0.144)</b>	<b>0.00</b>	<b>0.111 (<math>\pm</math>0.045)</b>	<b>(0.022; 0.199)</b>	<b>0.00</b>	<b>0.126 (<math>\pm</math>0.057)</b>	<b>(0.014; 0.238)</b>
Year * Prop_Sedim	<b>0.03</b>	<b>0.121 (<math>\pm</math>0.034)</b>	<b>(0.053; 0.188)</b>	<b>0.00</b>	<b>0.206 (<math>\pm</math>0.055)</b>	<b>(0.098; 0.315)</b>	<b>0.08</b>	<b>0.176 (<math>\pm</math>0.067)</b>	<b>(0.045; 0.307)</b>
Year * Thick_Sedim	0.12	0.054 ( $\pm$ 0.032)	(-0.009; 0.116)	<b>0.89</b>	<b>0.125 (<math>\pm</math>0.050)</b>	<b>(0.027; 0.224)</b>	0.35	0.076 ( $\pm$ 0.062)	(-0.046; 0.197)

Year * Dura_Inund	<b>0.39</b>	<b>-0.131 (±0.034)</b>	<b>(-0.198; -0.065)</b>	<b>0.00</b>	<b>-0.175 (±0.051)</b>	<b>(-0.276; -0.074)</b>	<b>0.05</b>	<b>-0.200 (±0.065)</b>	<b>(-0.328; -0.073)</b>
Year * Inte_Inund	0.00	-0.070 (±0.040)	(-0.148; 0.008)	<b>0.00</b>	<b>-0.236 (±0.060)</b>	<b>(-0.354; -0.118)</b>	0.00	-0.132 (±0.075)	(-0.279; 0.014)

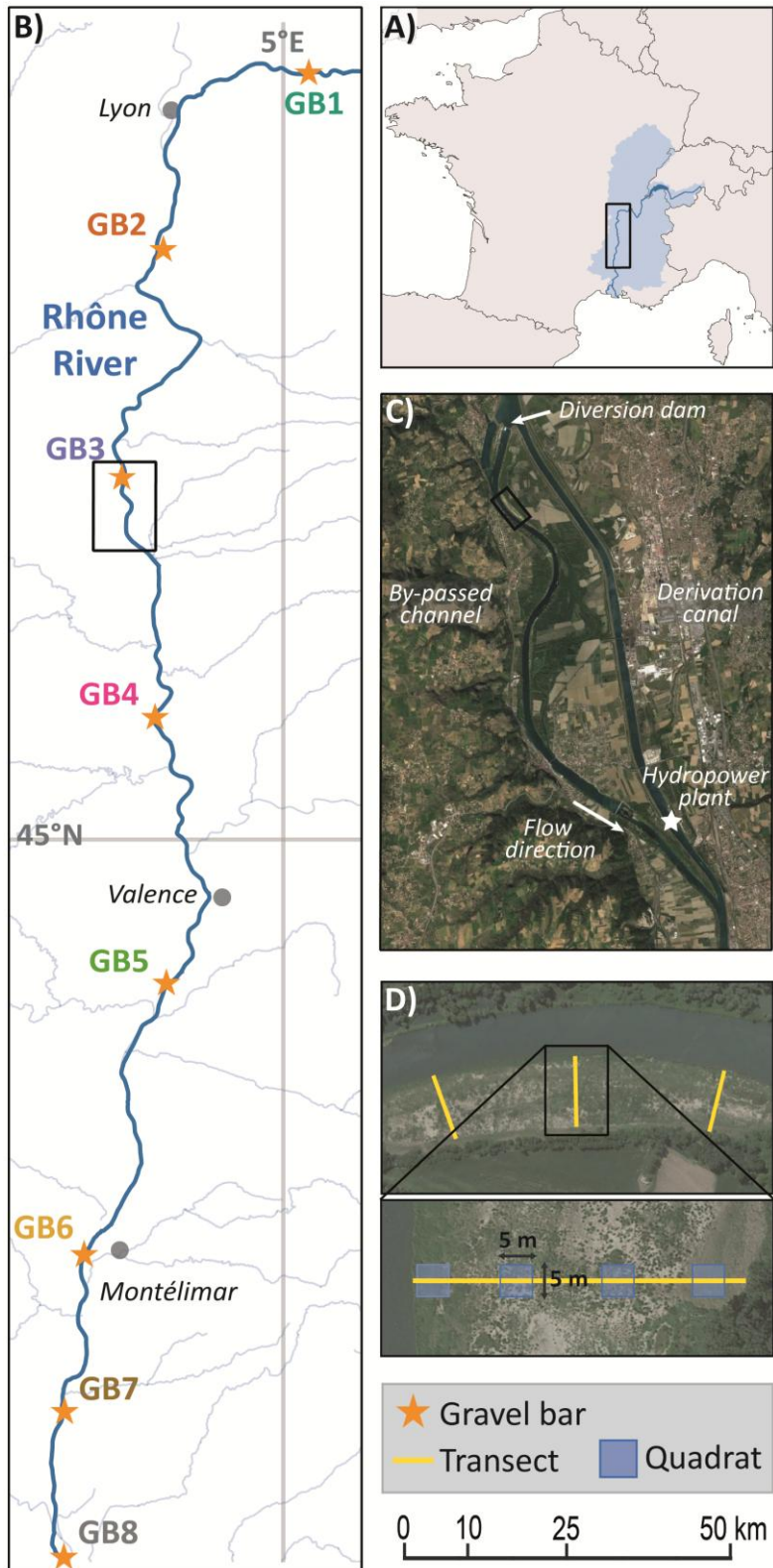
Parameters	FDis SLA			FDis Height			FDis seed		
	Imp.	Estimate (±SE)	(95% CI)	Imp.	Estimate (±SE)	(95% CI)	Imp.	Estimate (±SE)	(95% CI)
Year	1.00	-0.030 (±0.036)	(-0.100; 0.040)	1.00	-0.014 (±0.037)	(-0.086; 0.058)	1.00	-0.021 (±0.032)	(-0.084; 0.042)
Management	1.00	-0.013 (±0.087)	(-0.184; 0.158)	1.00	-0.048 (±0.038)	(-0.122; 0.026)	<b>1.00</b>	<b>0.164 (±0.076)</b>	<b>(0.014; 0.314)</b>
Elevation	<b>0.09</b>	<b>-0.090 (±0.026)</b>	<b>(-0.140; -0.039)</b>	0.00	-0.003 (±0.023)	(-0.048; 0.042)	0.03	0.014 (±0.028)	(-0.040; 0.068)
Distance	0.00	-0.042 (±0.025)	(-0.091; 0.007)	0.00	-0.004 (±0.026)	(-0.055; 0.047)	0.01	0.012 (±0.019)	(-0.025; 0.050)
Prop_Sedim	<b>0.20</b>	<b>-0.104 (±0.025)</b>	<b>(-0.152; -0.056)</b>	<b>0.79</b>	<b>-0.064 (±0.021)</b>	<b>(-0.105; -0.022)</b>	0.08	-0.039 (±0.025)	(-0.087; 0.009)
Thick_Sedim	<b>0.22</b>	<b>-0.106 (±0.025)</b>	<b>(-0.155; -0.056)</b>	<b>0.19</b>	<b>-0.056 (±0.022)</b>	<b>(-0.099; -0.013)</b>	0.82	-0.049 (±0.028)	(-0.105; 0.006)
Dura_Inund	<b>0.49</b>	<b>0.128 (±0.035)</b>	<b>(0.059; 0.197)</b>	0.01	0.024 (±0.024)	(-0.023; 0.071)	0.01	0.000 (±0.026)	(-0.051; 0.052)
Inte_Inund	<b>0.00</b>	<b>0.069 (±0.025)</b>	<b>(0.020; 0.118)</b>	0.00	0.001 (±0.021)	(-0.040; 0.042)	0.03	-0.030 (±0.026)	(-0.080; 0.021)
Year * Elevation	0.04	0.046 (±0.035)	(-0.021; 0.114)	0.00	0.024 (±0.038)	(-0.051; 0.098)	0.02	-0.064 (±0.033)	(-0.128; 0.000)
Year * Distance	0.00	0.046 (±0.036)	(-0.024; 0.117)	0.00	0.049 (±0.038)	(-0.025; 0.123)	0.00	0.002 (±0.033)	(-0.062; 0.066)
Year * Prop_Sedim	0.06	0.026 (±0.035)	(-0.043; 0.096)	0.22	0.017 (±0.037)	(-0.055; 0.090)	0.03	-0.031 (±0.033)	(-0.096; 0.034)
Year * Thick_Sedim	0.06	0.013 (±0.035)	(-0.055; 0.082)	0.05	0.016 (±0.037)	(-0.057; 0.089)	0.41	-0.048 (±0.032)	(-0.111; 0.015)
Year * Dura_Inund	<b>0.37</b>	<b>-0.075 (±0.036)</b>	<b>(-0.145; -0.005)</b>	0.00	-0.021 (±0.039)	(-0.098; 0.055)	0.00	0.037 (±0.034)	(-0.030; 0.105)

Year \* Inte\_Inund    0.00    0.027 ( $\pm 0.043$ )    (-0.057; 0.111)    0.00    0.012 ( $\pm 0.045$ )    (-0.076; 0.099)    0.02    0.071 ( $\pm 0.039$ )    (-0.007; 0.148)

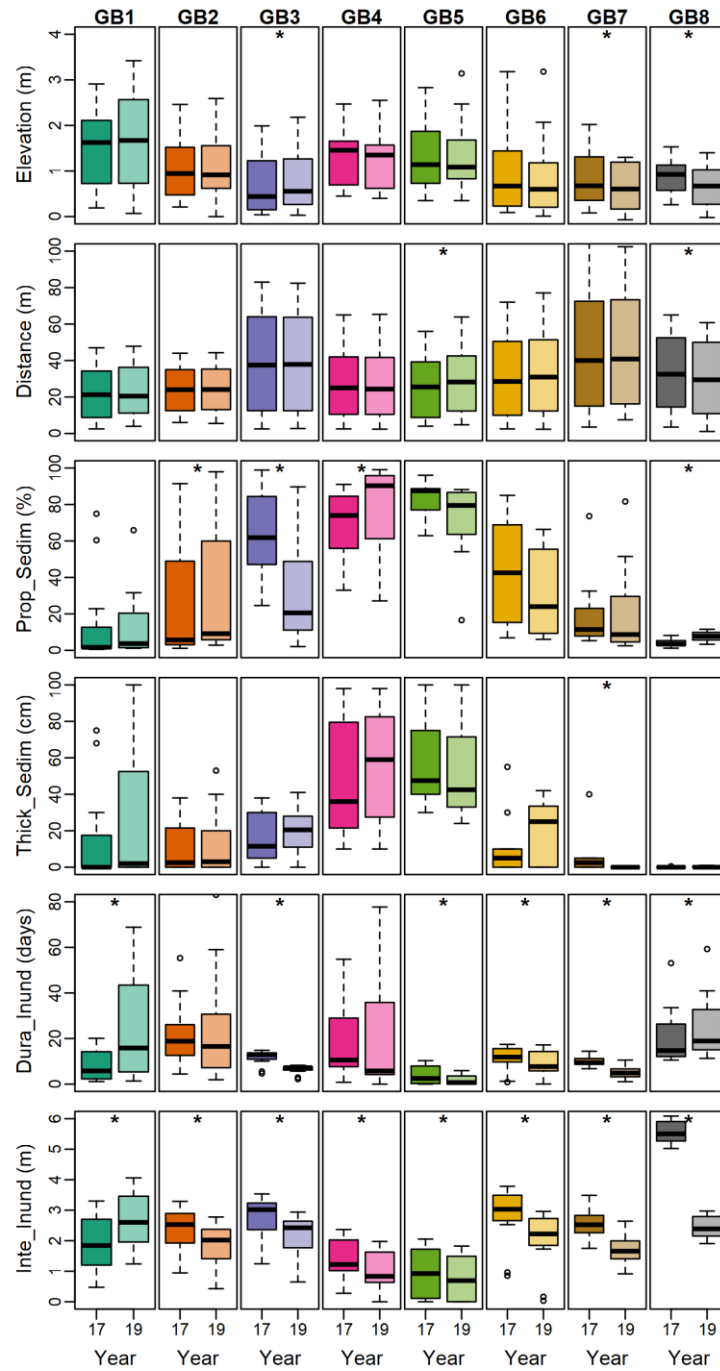
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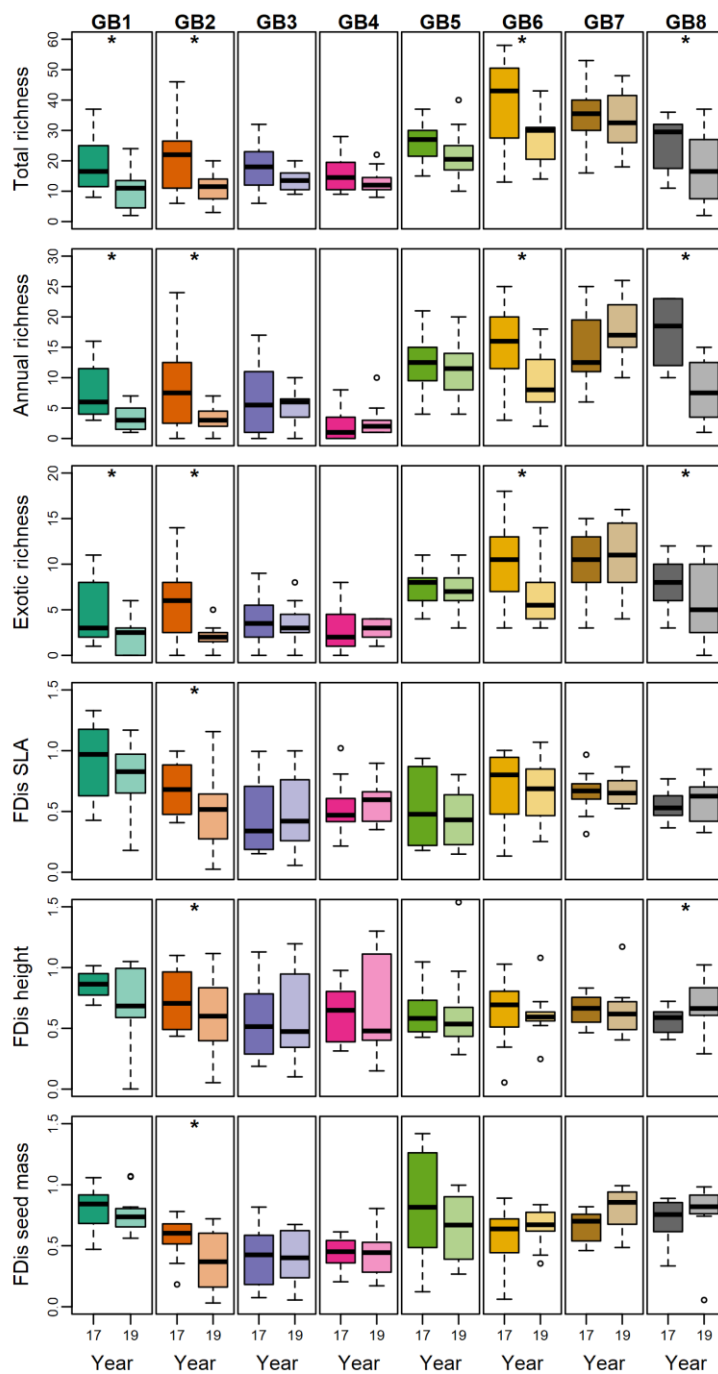
690 **Figure 1.** Location of the study area within the Rhône River watershed (A), distribution of sampled gravel bars  
 691 along the Rhône River corridor (B), typical arrangement of a diversion scheme on the Rhône (C) and form of the  
 692 sampling design used to survey riparian plant communities (D)



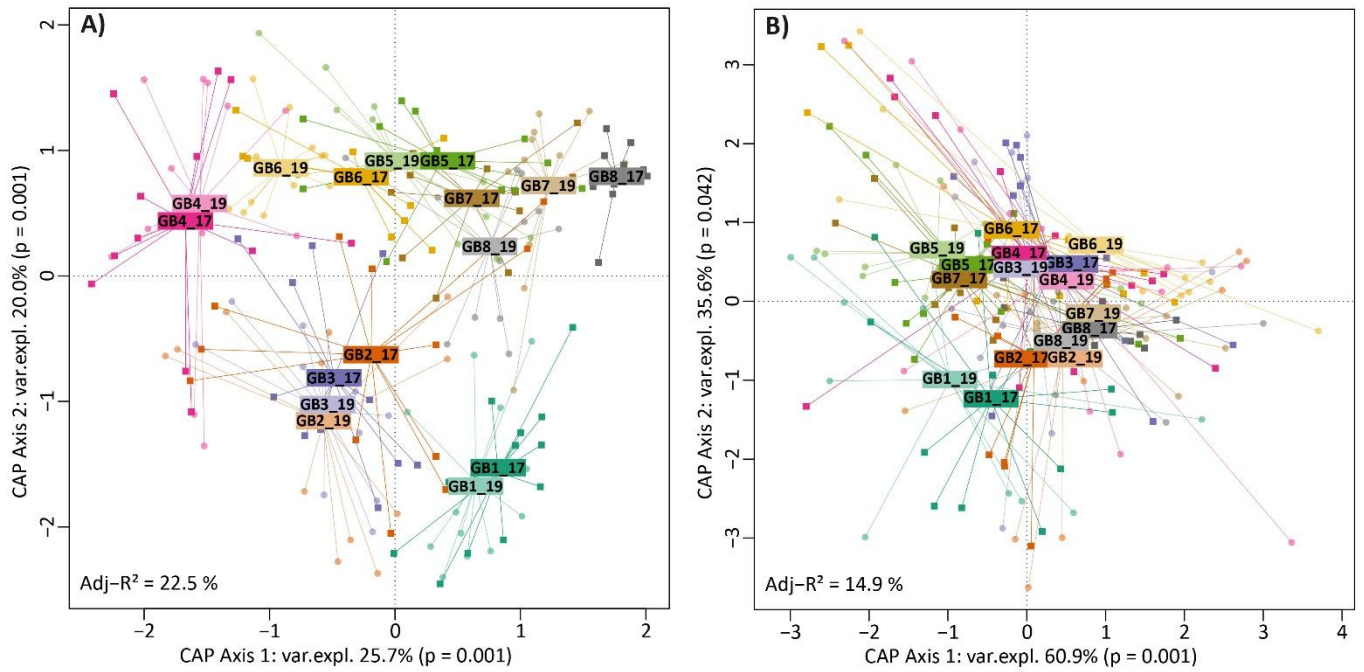
693 **Figure 2.** Variation in topographic, pedological and hydrological variables, for each gravel bar, between 2017  
 694 and 2019 along the Rhône River, France (\* = adjusted  $p$ -value < 0.05 based on paired samples  $t$ -test, see  
 695 Appendix S7 for details and refer to Table 1 for the description of the variables). Gravel bars are aligned in a  
 696 north-south direction of the river corridor (Figure 1), with GB1 to GB4 managed by brush clearing and GB5 to  
 697 GB8 managed by plowing



698 **Figure 3.** Variation in taxonomic and functional diversity of riparian plants, for each gravel bar, between 2017  
 699 and 2019, along the Rhône River, France (\* = adjusted  $p$ -value < 0.05 based on paired samples  $t$ -test, see  
 700 Appendix S9 for details and refer to Table 1 for the description of the variables). Gravel bars are aligned in a  
 701 north-south direction of the river corridor (Figure 1), with GB1 to GB4 managed by brush clearing and GB5 to  
 702 GB8 managed by plowing (FDis = functional dispersion)



703 **Figure 4.** Constrained canonical analysis of principal coordinates of A) taxonomic and B) functional composition  
 704 of riparian communities, for each gravel bars, between 2017 and 2019 along the Rhône River, France. Small  
 705 squares and circles represent the position of riparian communities at the quadrat scale, respectively in 2017  
 706 and 2019, colored lines connect each quadrat to the centroids in the principal coordinate space of each  
 707 individual bar per year, represented by a rectangle with the site name



708 **Figure 5.** Constrained canonical analysis of principal coordinates of A) taxonomic and B) functional composition  
 709 of riparian communities in relation to topographic, pedological and hydrological variables along the Rhône  
 710 River, France (refer to Table 1 for the description of the variables). To facilitate graphical interpretation, the  
 711 centroids in principle coordinate space of each individual bar by year, the 10 most abundant species and the  
 712 three functional traits (i.e., CWM) are provided

