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1 **How maintenance and restoration measures mediate the response of riparian plant**  
2 **functional composition to environmental gradients on channel margins: Insights from a**  
3 **highly degraded large river.**

4

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19

20 Running head: Human activity shapes riparian plants

21 **ABSTRACT**

22 Riparian habitats are transitional zones where strong environmental gradients shape  
23 community. To prevent flood risks and channel migration on managed rivers, civil  
24 engineering techniques have been widely used. Recently, ecological restoration of rivers has  
25 become a major issue. However, given the alteration of natural disturbance regimes induced  
26 by human infrastructures, the real added-value of these restoration actions is questionable.  
27 Thus, a major challenge is to better understand whether changes in abiotic conditions induced  
28 by human activity influence the response of plant communities to environmental gradients.  
29 Studying a highly degraded large river, we evaluated the effect of the elevation and soil  
30 texture gradients on plant functional composition and assessed whether human-mediated  
31 environment gradients, achieved through maintenance and restoration measures, shape  
32 community structure. In the summer of 2017, we sampled 17 geomorphic surfaces, mostly  
33 gravel bars, along the Rhône River and its tributaries that were either repeatedly cleared  
34 (brush clearing vs plowing), newly reprofiled or naturally rejuvenated by high flows. The  
35 results show shifts in trait values with elevation and convergence in plant traits with  
36 increasing proportion of fine sediments. The co-occurrence of species with contrasting traits  
37 was higher in highly disturbed environments, revealing the importance of rejuvenation  
38 processes. However, the influence of both environmental gradients was mediated by human  
39 activity. For maintenance measures, plowing was better able to promote species diversity and  
40 limited biotic homogenization along environmental gradients. Among the three geomorphic  
41 surfaces, naturally rejuvenated bars were the most stressful environments, hosting distinct  
42 functional assemblages, while communities on newly reprofiled banks were in the same  
43 ecological trajectories as repeatedly cleared bars. To promote an effective ecological  
44 restoration of riparian zones, (i) a greater variability of the minimum flow is needed, (ii)

45 bedload transport restoration should be a priority and (iii) reprofiled banks should better  
46 mimic the landforms of natural river margins.

47

48 **KEY WORDS**

49 Biodiversity conservation, community structure, ecological restoration, environmental  
50 gradient, trait-based approach, riparian zone

## 51        **1. INTRODUCTION**

52    At the interface between terrestrial and freshwater habitats, riparian zones represent a narrow  
53    portion of the landscape with disproportionate ecological importance, extending largely  
54    beyond their area (González et al., 2017). Indeed, riparian zones are dynamic ecosystems  
55    where the joint action of the flow and sediment regimes lead to great variability in habitat  
56    geomorphology (Naiman et al., 2005; Poff et al., 1997), which induce rapid changes in  
57    environmental conditions along the elevation gradient (Naiman and Decamps, 1997). Thus,  
58    from the lower to the upper part of banks, variations in soil moisture and inundation regime  
59    drives plant species turnover, i.e., from anoxic-tolerant species to species that tolerate periodic  
60    soil desiccation, and shape functional composition, i.e., from ruderal life strategy to  
61    competitor life strategy (Bejarano et al., 2017; Dawson et al., 2017; McCoy-Sulentic et al.,  
62    2017). Beside variations in species and traits composition along the elevation gradient, it has  
63    been shown that variations in soil texture are also of particular importance in explaining the  
64    functional composition of riparian plant communities (Kyle and Leishman, 2009; Xiong et al.,  
65    2001). Indeed, at low elevation level, an increase in the proportion of fine sediments may  
66    facilitate the establishment success of competitive species, leading to different patterns of  
67    species distribution along the flood gradient. The joint action of both the elevation and the soil  
68    texture gradients thus appears to have great importance in shaping riparian biodiversity.  
69    Worldwide riparian zones have been impacted by human activity (Feld et al., 2011; Nilsson et  
70    al., 2005). Civil engineering techniques have been widely used to control flood risks and  
71    prevent channel migration, which has greatly contributed to altering the flow and sediment  
72    regimes and, consequently, the ecological integrity of riparian zones (Poff and Zimmerman,  
73    2010). Moreover, in highly modified large rivers, vegetation encroachment is a significant  
74    adjustment process (Comiti et al., 2011; Liébault and Piégay, 2002), and it is sometimes  
75    prevented through vegetation maintenance and clearing to maintain wide low-roughness

76 channels and control flooding risks (Shields and Nunnally, 1984). All together, these human-  
77 induced changes have greatly altered the composition of riparian plant communities, leading  
78 to a loss in biodiversity (Bejarano et al., 2017; Biswas and Mallik, 2010; Poff et al., 2007).  
79 Specifically, by limiting rejuvenation processes, i.e., bedload supply and bank erosion due  
80 related to flood events as well as reduction of peak flow magnitude and frequency, these  
81 regulation measures have promoted a greater uniformity of environmental conditions with the  
82 risk of increased the taxonomic and functional similarities of riparian communities over times  
83 (i.e., biotic homogenization, Olden and Rooney, 2006).

84 To improve habitat and water quality along riparian zones, restoration efforts have become a  
85 major issue in European countries (Gumiero et al., 2013). Through bank reprofiling following  
86 dike and riprap removal or set-back, river managers aimed to recreate young patches and  
87 potentially stimulate alluviation/rejuvenation processes within the riverbed (Biron et al., 2014;  
88 Rohde et al., 2005). These measures are expected to increase riparian habitat heterogeneity  
89 (e.g., substrates, resources) and allows for a greater diversity of plant species. Moreover,  
90 despite their primary hydraulic objectives, maintenance measures are often viewed by river  
91 managers as a way to increase the ecological value of riparian zones, e.g., by favoring  
92 ecological succession and maintaining pioneer communities. However, given the irreversible  
93 alteration of the natural disturbance regimes of most rivers and modifications to biotic and  
94 abiotic conditions induced by human infrastructures (Poff et al., 1997; Richardson et al.,  
95 2007), the real ecological added value of these actions is questionable. Indeed, ecological  
96 communities of degraded riparian zones may have already been oriented toward transient or  
97 new states (Bunn and Arthington 2002, Richardson et al. 2007), making the return to the  
98 reference state difficult or impossible (Hobbs et al. 2009). From this view, it is thus of great  
99 concern to better understand whether maintenance and restoration measures influence the  
100 response of riparian plant communities to environmental gradients.

101 Here, we aimed to study the effect of the elevation and soil texture gradients on riparian plant  
102 functional composition. The elevation gradient was considered a proxy for flood duration,  
103 which is hypothesized to be the main disturbance controlling plant distributions in riparian  
104 zones (e.g., Fraaije et al., 2015; McCoy-Sulentic et al., 2017). The soil texture gradient was  
105 considered a proxy for soil moisture and fertility, which is hypothesized to be of great  
106 importance in structuring the functional composition of riparian plant communities (e.g., Kyle  
107 and Leishman, 2009; Xiong et al., 2001). Using a highly degraded river system, the Rhône  
108 River, as a case study, we further aimed to understand how human-mediated environmental  
109 gradients shape community structure. This result was achieved by evaluating the added value  
110 of maintenance and restoration measures applied along the Rhône River for the conservation  
111 of riparian biodiversity.

112 To date, few studies have used a functional approach to study assemblage patterns of riparian  
113 plants (Kyle and Leishman, 2009), particularly in the field of riparian vegetation restoration  
114 (González et al., 2015). However, unlike classical measures of species diversity, species traits  
115 capture different aspects of species' resource use and habitat requirements and are thus useful  
116 measures in unraveling complex patterns linking environmental changes, assemblage  
117 structures and ecosystem processes (Lavorel et al., 2008). By moving beyond species identity,  
118 trait-based approaches also enable comparisons of communities across systems (Cadotte et al.,  
119 2011), which allows to better evaluate successes or failures in restoration projects and thus  
120 better generalize research results. Moreover, in riparian zones, most of the previous studies  
121 using a functional approach have focused on a single environmental gradient, the flood  
122 gradient (Bejarano et al., 2017; McCoy-Sulentic et al., 2017), with little to no attention to the  
123 effects of interactions between it and other environmental gradients and/or human-mediated  
124 environmental gradients (but see, Brummer et al., 2016; Dawson et al., 2017). To accurately

125 define guidelines for the management and restoration of degraded riparian zones, this  
126 information is essential.

127 Specifically, we tested whether the mean and dispersion of selected trait values were  
128 influenced by the elevation and soil texture gradients as well as by maintenance and  
129 restoration measures on a range of riparian geomorphic surfaces (i.e., from gravel bars to  
130 channel banks). Analytical strategies that combine measures of the mean and dispersion of  
131 traits within a given species assemblage have been shown to describe two complementary  
132 aspects of the relationship between community structure and ecosystem functioning (de Bello  
133 et al., 2013; Ricotta and Moretti, 2011): (i) shifts in trait values due to environmental selection  
134 and (ii) patterns of trait convergence or divergence due to niche differentiation. Taking  
135 advantage of the large trait databases available currently (Kattge et al., 2011; Kleyer et al.,  
136 2008), we focused on three sets of traits widely used in riparian plant community studies (e.g.,  
137 Bejarano et al., 2017; Dawson et al., 2017; Kyle and Leishman, 2009) and describing crucial  
138 dimensions of plant growth requirements as well as major axes of plant functional strategies  
139 (Ellenberg et al., 1992; Westoby, 1998). We then assessed the response of plant functional  
140 composition to environmental gradients among three types of geomorphic surfaces –  
141 repeatedly cleared, i.e., relict bars along the Rhône River maintained by brush clearing or  
142 plowing, newly reprofiled, i.e., banks reprofiled following dike removal and naturally  
143 rejuvenated, i.e., reference river margins, – and addressed the following two questions: (i)  
144 how do elevation and soil texture gradients shape riparian plant functional composition along  
145 a highly degraded large River?; (ii) How does human activities, achieved through  
146 maintenance and restoration measures, influence the response of plant functional composition  
147 to environmental gradients?

148

## 149 **2. MATERIALS & METHODS**



## 2.1. Study area and experimental design

The study was carried out along the Rhône River (total length = 810 km, catchment area = 96,500 km<sup>2</sup>, mean annual discharge = 1,700 m<sup>3</sup>/s) in its French middle reach (approximately 250 km long) and three tributary rivers (Ain, Drôme and Doux Rivers, Figure 1). This area is characterized by a temperate climate with mean annual temperatures and precipitations of 13.6°C and 755 mm in the southern part and 11.6°C and 815 mm in the northern part. Within the study area, the Rhône River has been highly modified due to two historical development phases. During the 19<sup>th</sup> century, a rectification phase characterized by the building of a vast system of longitudinal submersible and transversal dikes in the main channel was carried out to facilitate navigation. In the second half of the 20<sup>th</sup> century, a derivation phase characterized by the construction of a series of lateral canals, running parallel to the natural Rhône River channel, was carried out to produce hydropower and facilitate irrigation and navigation. The bypassed sections, corresponding nowadays to part of the historical Rhône River channel, have been significantly impacted by the two phases, including changes in hydrological regime, channel dewatering, incision and lateral stabilization. They are characterized by a minimum flow that is observed most of the year, until the hydropower plant capacity is reached. Above this threshold, flood peaks are conveyed in the bypassed sections. Due to the peak-flow decrease, bedload supply interruption and associated bedload coarsening following gravel winnowing and bed armouring, no bedload transport is observed along most of these channels. Taken together, these hydro-morphological modifications have profoundly impoverished aquatic and terrestrial habitats. Since 2000, bypassed section have been subject to an ambitious ecological restoration program that mainly involves cut-off secondary channel dredging and reconnection and minimal flow increases (Lamouroux et al., 2015). In summer 2017, we sampled 17 geomorphic surfaces (mostly gravel bars that were somewhat subject to fine-grained overbank alluviation) that we classified into three types:

175 relict bars that were repeatedly cleared (n = 9), newly reprofiled banks (n = 4) and naturally  
176 rejuvenated bars (n = 4) (Figure 1). Relict bars are usually fixed in bypassed sections of the  
177 Rhône riverbed, i.e., coarse sediments are no longer remobilized during flood events and are  
178 subject to fine-grained overbank sedimentation and colonization by trees. These large fixed  
179 gravel bars correspond to a part of the river bottom before derivation and represent the only  
180 terrestrial habitats available for species within the Rhône riverbed. To prevent encroachment  
181 by trees and shrubs of these surfaces and associated channel narrowing, maintenance  
182 measures are implemented by river managers to scrap them by either brush clearing (n = 4) or  
183 plowing (n = 5). Reprofiled banks are newly restored surfaces due to bank reprofiling  
184 following dike removal in bypassed sections of the Rhône riverbed. These engineering actions  
185 were performed to widen the channel for improving flow conveyance. These new surfaces are  
186 not paved, with soil texture and topographical features quite comparable to those of  
187 repeatedly cleared bars. They represent new available terrestrial habitats for species  
188 colonization within the Rhône riverbed. These actions have been conducted on four reaches  
189 (one in 2009, one in 2015 and two in 2017) belonging to two bypassed sections. They are  
190 intended to be progressively eroded to promote self-gravel augmentation, bedload transport  
191 and new natural rejuvenated bar creation downstream. Naturally rejuvenated bars are still  
192 actively mobile bars in terms of bedload supply and erosion and are thus subject to bedload  
193 alluviation/rejuvenation processes, i.e., coarse sediments are partially remobilized during  
194 flood events. In the study area, such surfaces are mostly restricted to tributary rivers (Ain,  
195 Drôme and Doux Rivers), although a few bars of the Rhône riverbed are currently naturally  
196 rejuvenated because of existing bedload transport (e.g., Miribel reach, upstream of Lyon).  
197 These bars are considered natural reference geomorphic surfaces and are features that could  
198 potentially be restored in some of the bypassed sections.

## 199 **2.2. Vegetation data**

200 On each geomorphic surfaces, vegetation was surveyed along three transects spaced at a  
201 distance of approximately 100 m from each other (Figure 1). Transects were positioned  
202 perpendicularly to the river, in areas with clear elevation gradients relative to the water  
203 surface (means  $\pm$ SD = 1.17  $\pm$ 0.93 m; range = 0.04-6.20 m). The transect length varied from  
204 30 m to 105 m, depending on the length of the local gradient. They started directly from the  
205 water line and ended before the alluvial floodplain, which was mostly occupied by riparian  
206 forest. Along each transect, four 5 x 5 m quadrats (25 m<sup>2</sup>) were positioned, for a total of 12  
207 quadrats per geomorphic surface. Quadrats were positioned in visually homogenous  
208 topographical and pedological areas, while avoiding aquatic parts of the river margin and  
209 targeting similar plant communities. Within each quadrat (n = 204), all vascular plants were  
210 surveyed following the Braun-Blanquet abundance-dominance methodology. Because  
211 geomorphic surfaces along the Rhône River were repeatedly cleared, tree and shrub layers  
212 were systematically absent and vegetation surveys were conducted by considering the  
213 herbaceous layer only. To characterize the entire plant community and account for plant  
214 phenology, two complete surveys were conducted (June and July 2017) and to limit observer  
215 biases, all surveys were performed by the first author (PJ).

### 216 **2.3. Trait data**

217 We used three groups of plant traits. Three ecological traits – plant species preferences for  
218 light, nitrogen content and soil moisture – were extracted from the Baseflor database (Julve,  
219 1998), and the few missing values (n species = 22) were filled by using the ecological  
220 information of closely related species, i.e., same genus. These ecological traits, i.e.,  
221 Ellenberg's indicator values (Ellenberg et al., 1992), were used to characterize variations in  
222 species habitat niches along environmental gradients and to highlight whether maintenance  
223 and restoration measures modify abiotic conditions along river margins. Three morphological  
224 traits – specific leaf area (SLA), plant height at maturity and seed mass – were extracted from

225 the TRY database (Kattge et al. 2011), and we calculated a mean trait value per species from  
226 them after removing all values with an error risk  $> 3$  (see also A.1). For missing values, data  
227 were completed using the LEDA database (Kleyer et al., 2008) and, in a few cases ( $n$  species  
228 = 6), by using the information available for closely related species i.e., same genus. Within  
229 Westoby's L-H-S scheme (Westoby, 1998), SLA is related to resource acquisition and  
230 conservation, height at maturity to competitive ability and seed mass to dispersal ability.  
231 Three groups of species – annual, hydrochorous and alien species – were identified from the  
232 LEDA (annual species) and Baseflor databases (hydrochorous and alien species). Annual  
233 species characterize pioneer communities which are targeted by restoration measures along  
234 the Rhône River; hydrochorous species are dispersal-specialized species of high importance in  
235 riparian plant communities which are sensitive to alteration of the flow regime (Nilsson et al.,  
236 2010); alien species, defined as introduced species originated from America, Africa and Asia  
237 (i.e., based on species chorology), represent potential threats to native riparian plant  
238 communities which pose challenges in restoration measures (Richardson et al., 2007).  
239 Overall, these three species groups were used to highlight how environmental gradients drive  
240 changes in riparian zones diversity patterns and to assess whether maintenance and restoration  
241 measures affect these patterns.  
242 For each trait value, we computed community-weighted means (CWM) and functional  
243 dispersion (FDis). CWM is defined as the mean of trait values weighted by the relative  
244 abundance of each species bearing each value (Lavorel et al., 2008). FDis is defined as the  
245 mean distance of individual species to the weighted centroid of all species in the assemblage  
246 (Laliberté and Legendre, 2010). For each species group, we computed the total species  
247 richness and cover.

#### 248 **2.4. Elevation and soil texture gradients**

249 At the center of each quadrat, the elevation difference to the water line was characterized  
250 using topographical surveys. Topographical measurements were conducted using a laser  
251 rangefinder (TruPulse 200X) positioned on a tripod at a constant height of 1.20 m and a target  
252 at a height of 2 m. The horizontal distance between the tripod and the target was taken from  
253 the water line at the beginning of each transect and the center of the four successive quadrats.  
254 Soil properties were derived from two soil core samples (30-cm depth) collected in two  
255 representative areas within each quadrat and pooled together. Each composite soil sample was  
256 then dried, weighed and sieved at the laboratory to estimate the proportion of large (>0.2-mm  
257 mesh), medium (>50- $\mu$ m mesh) and fine (<50- $\mu$ m mesh) sediments. Due to the high  
258 correlation between these three variables and to avoid multicollinearity issues, we focused on  
259 only the proportion of subsoil fine sediments in subsequent analysis. This variable was  
260 preferred over others because it was considered the most meaningful variable to represent the  
261 process of fine-grained sediment alluviation that affects several gravel bars along the Rhône  
262 River.

## 263 **2.5. Statistical analysis**

264 Analyses were performed with R version 3.4.2 (R Core Team, 2017). Continuous independent  
265 variables were the elevation difference (denoted “elevation” in tables and figures) and the  
266 proportion of fine sediments (denoted “fine\_sediments”); independent factors were  
267 maintenance measures, i.e., brush clearing vs plowing (denoted “maintenance”), and  
268 geomorphic surface type, i.e., repeatedly cleared relict bars vs newly reprofiled banks vs  
269 naturally rejuvenated bars (denoted “type”). Because independent variables were measured on  
270 different scales and because we were interested in interpreting the main effects of continuous  
271 variables in the presence of interactions, input variables were centralized (Schielzeth, 2010).  
272 Dependent variables were the CWM and the FDis of ecological and morphological trait  
273 values as well as the pooled richness and the cover of species groups at each quadrat. Because

274 the seed mass of a few species was very large, this trait value was log-transformed before  
275 CWM and FDis calculations. We then used one-way ANOVA with a type III sum of squares  
276 to determine if the elevation difference and the proportion of fine sediments varied differently  
277 between maintenance measures and among geomorphic surface types (car package).  
278 To determine whether human-mediated environment gradients shape the functional  
279 composition of riparian plants we used an analytical strategy involving two steps. First, by  
280 using quadrats located on only repeatedly cleared relict bars of the Rhône River (n = 108), we  
281 sought to understand whether environmental gradients shape riparian plant communities along  
282 a highly degraded large River and whether maintenance measures influence the response of  
283 plant functional composition to environmental gradients. Second, by using the whole dataset  
284 (n = 204), we sought to understand whether the response of plant functional composition to  
285 environmental gradients vary among repeatedly cleared relict bars, newly reprofiled banks of  
286 the Rhône riverbed and naturally rejuvenated bars, mostly sampled on tributary rivers (natural  
287 reference).

288 2.5.1. How do environmental gradients and maintenance measures shape plant functional  
289 composition along the Rhône River?

290 We considered 13 a priori models testing the main and interaction effects between the  
291 elevation and soil texture gradients and between environmental gradients and maintenance  
292 measures plus the null model (A.2.1). Because we used a nested sampling design in which  
293 “quadrats” were not really replicated along “transects” and “banks”, we used linear mixed  
294 models (LMMs, lme4 package) in which “transects” and “banks” were included as random  
295 effects. For continuous dependent variables (i.e., trait values), we fitted normal LMMs or log-  
296 normal LMMs for skewed response variables (i.e., plant height). For count dependent  
297 variables (i.e., richness and cover), to avoid statistical issues linked to overdispersion, we  
298 fitted negative binomial distribution general linear mixed models (GLMMs, lme4 package). In

299 all candidate models, the variance inflation factor was below five, indicating a lack of  
300 collinearity issues (Dormann et al., 2013). The variance explained by LMMs and GLMMs  
301 was estimated using the marginal coefficient of determination for fixed effect parameters  
302 alone (Nakagawa and Schielzeth, 2013). To identify the most parsimonious regression model,  
303 we used Akaike's information criterion corrected for small sample sizes (Burnham and  
304 Anderson, 2002). To estimate parameters and associated unconditional standard errors, we  
305 used model averaging based on the subset of top ranking models for which  $\Delta AICc < 2$   
306 (MuMin package).

307 2.5.2. How does the response of plant functional composition to environmental gradients vary  
308 among geomorphic surface types?

309 We considered 13 a priori models testing the main and interaction effects between both  
310 environmental gradients and between environmental gradients and geomorphic surface types  
311 plus the null model (A.2.2). In LMMs and GLMMs, the relict bar factor was set as the  
312 reference level. In all candidate models, the variance inflation factor was below five. The  
313 variance explained by models, models ranking and estimate of parameters and of  
314 unconditional standard errors were done in the same manner as previously (2.5.1.).

315

### 316 **3. RESULTS**

317 Overall, 273 plant species (mean  $\pm$ SD = 28  $\pm$ 13) were recorded on the 204 quadrats along the  
318 Rhône River and tributaries. Distinguishing between surface types: 203 species (28  $\pm$ 12) were  
319 recorded on repeatedly cleared relict bars (n = 108), with 142 species (32  $\pm$ 10) on surfaces  
320 maintained by brush clearing (n = 48) and 171 species (25  $\pm$ 13) on surfaces maintained by  
321 plowing (n = 60); 198 species (31  $\pm$ 13) were recorded on newly reprofiled banks (n = 48); and  
322 175 species (24  $\pm$ 13) were recorded on naturally rejuvenated bars (n = 48). Because  
323 ecological successions are blocked on repeatedly cleared relict bars, i.e., gravel bars are

324 scraped to avoid colonization by tree and shrub species, regeneration and seedling of tree  
325 species (n = 15) were removed from the dataset to avoid bias in the estimates of trait values  
326 (especially plant height at maturity). Subsequent analyses were thus conducted on a dataset of  
327 258 herbaceous plant species.

### 328 **3.1. How environmental gradients vary between maintenance measures and among** 329 **geomorphic surface types?**

330 On repeatedly cleared relict bars, ANOVAs showed that the variation in mean elevation and  
331 in the mean proportion of fine sediments was not related to maintenance measures (Figure 2,  
332 A.3 & A.4). This result indicates that in our study design, both environmental gradients varied  
333 consistently among geomorphic surfaces maintained by either brush clearing or plowing.

334 Between repeatedly cleared relict bars, newly reprofiled banks and naturally rejuvenated bars,  
335 ANOVAs showed no significant variations in the mean elevation. However, the proportion of  
336 fine sediments significantly differed between surface types (p-value < 0.001, Figure 2), which  
337 was due to the lower proportion of fine sediments on naturally rejuvenated bars (mean  $\pm$ SD,  
338  $3.99 \pm 7.47$ ) than on repeatedly cleared relict bars ( $15.90 \pm 16.42$ ) and newly reprofiled banks  
339 ( $14.20 \pm 10.71$ ).

### 340 **3.2. How do environmental gradients and maintenance measures shape plant** 341 **functional composition along the Rhône River?**

342 Results showed that variations in plant species preferences for soil moisture (mean and  
343 dispersion), light (dispersion) and nitrogen content (dispersion), in plant height (mean), seed  
344 mass (mean) and SLA (dispersion) trait values and in hydrochorous (richness and cover),  
345 annual (richness and cover) and alien (cover) species were best predicted by one of the a  
346 priori models (Table 1). The goodness of fit of these models varied from 14.6 % (dispersion  
347 of nitrogen content) to 51.7 % (hydrochorous species richness). However, for light (mean),  
348 nitrogen content (mean), SLA (mean), plant height (dispersion), seed mass (dispersion) and



349 alien species (cover), since the null model was either the top-ranked or part of top-ranked  
350 models (i.e.,  $\Delta AICc < 2$ ) none of the estimated parameters is of any inferential value.

### 351 ***3.2.1. Influence of environmental gradients***

352 Model averaging (Table 2) revealed that an increase in the elevation level induced decreases  
353 in mean soil moisture trait value, the dispersion of SLA trait values and hydrochorous species  
354 richness but an increase in mean seed mass trait value. An increase in the proportion of fine  
355 sediments induced decreases in the dispersion of soil moisture, nitrogen content and SLA trait  
356 values and in the richness and cover of annual species. Mean plant height, the dispersion of  
357 light trait values, the richness of alien species and the cover of hydrochorous species were  
358 influenced by the interaction between the elevation and soil texture gradients. Graphical  
359 interpretation (Figure 3) revealed that the mean plant height and cover of hydrochorous  
360 species were higher on gravel bars with high proportion of fine sediments and decreased less  
361 with elevation when the proportion of fine sediments was low. The dispersion of light trait  
362 values and richness of alien species decreased with elevation when the proportion of fine  
363 sediments was low but increased with elevation when the proportion of fine sediments was  
364 high.

### 365 ***3.2.2. Influence of maintenance measures***

366 Model averaging (Table 2) revealed that maintenance measures mediated the response of  
367 nitrogen content (dispersion) and SLA (dispersion) trait values and of annual species (richness  
368 and cover) to environmental gradients. Graphical interpretation (Figure 4) revealed that the  
369 dispersion of SLA trait values was higher on bars maintained by plowing and decreased less  
370 with elevation on bars maintained by brush clearing. The dispersion of nitrogen content trait  
371 values and annual species cover decreased with an increase in the proportion of fine  
372 sediments on bars maintained by brush clearing but did not change on those maintained by  
373 plowing. The richness of annual species was higher on bars maintained by plowing and

374 tended to decrease more with increasing proportion of fine sediments on bars maintained by  
375 brush clearing. Finally, alien species richness was higher on bars maintained by plowing.

### 376 **3.3. How does the response of plant functional composition to environmental** 377 **gradients vary among geomorphic surface types?**

378 Results showed that variations in plant species preferences for soil moisture (mean and  
379 dispersion), light (mean and dispersion) and nitrogen content (mean and dispersion), in SLA  
380 (mean and dispersion), plant height (mean) and seed mass (mean and dispersion) trait values  
381 and in hydrochorous (richness and cover), annual (richness) and alien (cover) species were  
382 best predicted by one of the a priori models (Table 3). The goodness of fit of these models  
383 varied from 3.7 % (dispersion of seed mass) to 56.0 % (mean soil moisture). However, for  
384 plant height (dispersion), alien (richness) and annual (cover) species, since the null model was  
385 either the top-ranked or part of top-ranked models (i.e.,  $\Delta AICc < 2$ ), none of the estimated  
386 parameters is of any inferential value.

#### 387 ***3.3.1. Influence of environmental gradients***

388 Model averaging (Table 4) revealed that an increase in the elevation induced a decrease in the  
389 dispersion of SLA trait values but an increase in mean light trait value and the dispersion of  
390 seed mass trait values, which was consistent among the three geomorphic surfaces. An  
391 increase in the proportion of fine sediments induced a decrease in the dispersion of soil  
392 moisture, nitrogen content and SLA trait values and in the richness of annual species but an  
393 increase in the cover of alien species, which was consistent among the three geomorphic  
394 surfaces. Mean plant height and dispersion for light trait values were influenced by the  
395 interaction between the elevation and soil texture gradients, i.e., mean plant height decreased  
396 with elevation when the proportion of fine sediments was high but increased when the  
397 proportion of fine sediments was low while the dispersion for light trait values decreased with

398 elevation when the proportion of fine sediments was low but increased when the proportion of  
399 fine sediments was high.

### 400 **3.3.2. *Influence of restoration measures***

401 Comparing the response of plant traits to environmental gradients between repeatedly cleared  
402 relict bars and newly reprofiled banks, model averaging (Table 4) revealed that soil moisture  
403 (mean), plant height (mean) and seed mass (mean) trait values and that hydrochorous  
404 (richness and cover) and alien (cover) species varied differently between the two geomorphic  
405 surfaces. Graphical interpretation (Figure 5-A) revealed that mean soil moisture trait value,  
406 mean plant height trait value and hydrochorous richness and cover decreased more rapidly  
407 with elevation on relict bars than on reprofiled banks. Mean seed mass trait value increased  
408 more rapidly with elevation on relict bars than on reprofiled banks. Alien cover was higher on  
409 reprofiled banks than on relict bars and tended to decrease more rapidly with elevation on  
410 reprofiled banks. Finally, mean light trait value was higher on reprofiled banks than on relict  
411 bars.

412 Comparing the response of plant traits to environmental gradients between repeatedly cleared  
413 bars and naturally rejuvenated bars, model averaging (Table 4) revealed that nitrogen content  
414 (mean), soil moisture (dispersion), SLA (mean), plant height (mean) and seed mass (mean and  
415 dispersion) traits values and that alien (cover) species varied differently between the two  
416 geomorphic surfaces. Graphical interpretation (Figure 5-B) revealed that mean nitrogen  
417 content, SLA and seed mass trait values decreased with elevation on naturally rejuvenated  
418 bars but increased on repeatedly cleared bars. Mean plant height increased with elevation on  
419 naturally rejuvenated bars but decreased on repeatedly cleared bars. The dispersion of soil  
420 moisture trait values decreased more rapidly with elevation level on naturally rejuvenated bars  
421 than on repeatedly cleared bars. Seed mass dispersion decreased more rapidly with proportion  
422 of fine sediments on naturally rejuvenated bars than on repeatedly cleared bars. Alien cover

423 was higher on naturally rejuvenated bars than on repeatedly cleared bars and tended to  
424 decrease less rapidly with elevation on naturally rejuvenated bars. Finally, the mean light trait  
425 value was higher, but the mean soil moisture trait value and hydrochorous species richness  
426 and cover were lower on naturally rejuvenated bars than on repeatedly cleared bars.

427

#### 428 **4. DISCUSSION**

429 Using a trait-based approach, which is rarely used in studies evaluating the success of  
430 restoration actions on riparian vegetation (González et al., 2015), we showed that (i) elevation  
431 and soil texture gradients have strong and sometimes interactive effects on plant functional  
432 composition and that (ii) the influence of both environmental gradients is mediated by human  
433 activity. The co-occurrence of species with contrasting resource requirements and  
434 morphological traits was higher in highly disturbed environments, i.e., on surfaces not subject  
435 to fine-grained overbank alluviation and hydrological disconnection. Rejuvenation processes,  
436 through natural or human-induced disturbances, thus appear essential to avoid biotic  
437 homogenization and promote habitat heterogeneity.

##### 438 **4.1. Both the elevation and the soil texture gradients shape riparian plant functional** 439 **composition**

440 In riparian zones of the Rhône River, shifts in ecological traits were highlighted in relation to  
441 both environmental gradients. The elevation gradient drives changes in the plant species  
442 habitat niche, emphasizing patterns of hydrological niche segregation (Silvertown et al.,  
443 2015). In line with previous studies (Auble et al., 1994; Fraaije et al., 2015; Garssen et al.,  
444 2017), this shift confirms the importance of the soil moisture gradient in shaping riparian  
445 plant communities. Conversely, the soil texture gradient was related to patterns of trait  
446 convergence, i.e., an increase in the proportion of fine sediments induced decreases in the  
447 dispersion of soil moisture and nitrogen content trait values. Also, low proportion of fine

448 sediments allowed for a better co-occurrence of species with contrasting light resource  
449 requirements, revealing a combination of xeric, mesic and hydric habitat conditions on gravel  
450 bars made of coarse sediments. This result suggests that continuous alluviation of fines leads  
451 to patterns of biotic homogenization (Olden and Rooney, 2006), underlining thus the  
452 importance of rejuvenation processes in increasing habitat heterogeneity (Steiger et al., 2005).  
453 Changes in the plant species habitat niche induced environmental selection toward specific  
454 plant morphological traits. In line with previous studies (Kyle and Leishman, 2009; McCoy-  
455 Sulentic et al., 2017), a shift in the mean seed mass trait value was highlighted along the  
456 elevation gradient, confirming that species with small seed masses have better potential to  
457 colonize disturbed environments than species with large seed masses (Gurnell et al., 2008).  
458 Moreover, the interaction between the elevation and soil texture gradients influenced mean  
459 plant height. Indeed, tall herb species, such as *Phragmites australis* and *Phalaris*  
460 *arundinacea*, were more frequently surveyed close to the water line on relict gravel bars  
461 subject to fine sediment alluviation. This relation may reflect the adaptation of plant species to  
462 fairly constant flow during the vegetative period due to the regulation of flood events in  
463 bypassed sections but also to the long-term decrease in bedload discharge, limiting the  
464 mortality of perennial plants by coarse bed scour and burial disturbances (e.g., Kui and Stella,  
465 2016; Polzin and Rood, 2006). Besides shifts in traits, patterns of trait  
466 convergence/divergence were highlighted. Along both the elevation and the soil texture  
467 gradients, SLA values converged, i.e., species with contrasting resource acquisition and  
468 conservation strategies co-occurred less at high elevation and on gravel bars subject to fine  
469 sediment alluviation, thus confirming patterns of biotic homogenization.  
470 Finally, diversity patterns of plant species groups were also influenced by both environmental  
471 gradients. A higher diversity of hydrochorous species occurred at low elevation level (Fraaije  
472 et al., 2017), while a higher diversity of annual species was related to a low proportion of fine

473 sediments (Corenblit et al., 2009). Additionally, our results showed that the elevation and soil  
474 texture gradients interacted to shape diversity patterns. Indeed, the richness of alien species  
475 was maximal at low elevation but tended to increase along the elevation gradient when the  
476 proportion of fine sediments was high (Brummer et al., 2016). This pattern shows that the  
477 effect of both environmental gradients on plant communities may not be independent and  
478 argues for a better consideration of the soil texture gradient in riparian vegetation studies  
479 (Kyle and Leishman, 2009). Since taxonomic and functional diversity peaked at low  
480 elevation, on geomorphic surfaces not subject to fine-grained sediment alluviation, i.e., in  
481 frequently flooded areas, our results show that greater disturbance of environments within the  
482 Rhône riverbed promotes a greater diversification of habitats that benefit a larger diversity of  
483 species with contrasting functional strategies. Rejuvenation processes thus appear essential to  
484 conserving or restoring the functionality of riparian communities in highly degraded rivers.

#### 485 **4.2. Patterns of biotic homogenization are mitigated on gravel bars maintained by** 486 **plowing**

487 Distinguishing between relict bars of the Rhône River maintained by either brush clearing or  
488 plowing, we found that shifts in ecological and morphological traits in relation to  
489 environmental gradients were consistent. However, along the elevation gradient, the  
490 dispersion of SLA trait values diverged more at low elevation on river margins maintained by  
491 plowing than on other geomorphic surfaces. Also, with increasing proportion of fine  
492 sediments, nitrogen content trait values converged on only bars maintained by brush clearing.  
493 Co-occurrence of species with similar ecological and morphological traits were thus more  
494 pronounced on bars maintained by brush clearing, indicating patterns of biotic  
495 homogenization. Reversely, deeply disturbing the soil surface increases habitat heterogeneity,  
496 by providing a larger diversity of environmental conditions (microsites, resources) and thus a  
497 greater diversity of habitat niches. Specifically, plowing permits the active remobilization of

498 fine sediments, favoring erosion processes at local scale and substrate heterogeneity, which  
499 better allows for the co-occurrence of species with contrasting trophic requirements and  
500 resource acquisition strategies. Plowing also mediated the response of annual species to the  
501 soil texture gradient by enabling the maintenance of a more cover on gravel bars subject to  
502 fine-grained overbank alluviation, and promoted larger species richness of annual but also of  
503 alien species. Consistently with previous studies (e.g., Catford et al., 2012; Nilsson et al.,  
504 1989), this pattern highlight that colonization opportunities for ruderal species, among which  
505 annual and alien herbaceous species are well represented, increase in frequently disturbed  
506 riparian zones, mostly because competition for limiting resources is minimal. Overall, those  
507 results underlined the importance of rejuvenation processes in riparian zones to support  
508 functional and species diversity (e.g., Biswas and Mallik, 2010). Specifically, our results  
509 indicated that plowing better promotes pioneer communities within the Rhône riverbed, but  
510 also alien species, and better limits biotic homogenization along environmental gradients.  
511 Given the current alteration of the natural disturbance regimes of the Rhône River (mainly bar  
512 scouring through bedload transport), it may be argued that plowing could be a potential  
513 compromise between hydraulic (i.e., maintain wide low-roughness channels) and ecological  
514 (i.e., promote pioneer communities) considerations. However, beyond the fact that plowing  
515 does not only promote native pioneer communities, the strong economic and environmental  
516 costs of this maintenance operation must also be considered. In this view, bedload transport  
517 restoration in bypassed sections should be promoted first as a sustainable management  
518 perspective (González et al., 2017).

519 **4.3. The response of plant functional composition to environmental gradients**  
520 **diverged between repeatedly cleared relict bars, newly reprofiled banks and**  
521 **naturally rejuvenated bars.**

522 Among the three geomorphic surface types, shifts in soil moisture and light requirement trait  
523 values with elevation and trait convergence for soil moisture and nitrogen content trait values  
524 with increasing proportion of fine sediments were consistent. However, strong differences in  
525 plant species habitat niches were also highlighted. Soil moisture trait values were lower on  
526 naturally rejuvenated bars than on other geomorphic surfaces and decreased less with  
527 elevation on newly reprofiled banks. Moreover, the abundance of full light-demanding species  
528 was higher on naturally rejuvenated and newly reprofiled surfaces than on repeatedly cleared  
529 relict bars. Thus, the environmental filtering from the lower to the upper part of river margins  
530 appears to be more stressful on naturally rejuvenated bars. This pattern is undoubtedly related  
531 to the low proportion of fine sediments on these surfaces and thus to the low water-holding  
532 capacity (Naiman and Decamps, 1997). Soil properties may also explain the shift in nitrogen  
533 content trait value along the elevation gradient that we found on only naturally rejuvenated  
534 bars. Indeed, the decrease in soil fertility (i.e., inferred from plant species trait values) with  
535 elevation may be related to both the low proportions of fine-grained overbank deposits at  
536 medium elevation and the young age of naturally rejuvenated bars, which thus prevent the  
537 establishment of the nitrogen-demanding species that are abundant on older relict bars (e.g.,  
538 *Artemisia vulgaris*, *Solanum nigrum*, *Sonchus oleraceus*). Finally, the convergence of soil  
539 moisture trait values highlighted along the elevation gradient on only naturally rejuvenated  
540 bars may result from higher environmental selection toward plant species with similar  
541 hydrological requirements, confirming that these natural reference bars encompass stressful  
542 environmental conditions.

543 As expected, differences in plant species habitat niches among the three surface types were  
544 related to shifts in plant morphological traits. Along the elevation gradient, mean plant height  
545 increased on naturally rejuvenated bars but decreased on repeatedly cleared relict bars and  
546 newly reprofiled banks. This underlines the importance of competition in bypassed sections



547 and confirms long periods of growth opportunity between disturbances. Additionally, our  
548 results indicate that the mean seed mass increased with elevation on relict bars and reprofiled  
549 banks but decreased with elevation on naturally rejuvenated bars. Considering the critical role  
550 played by flooding in shaping patterns of seed deposition along the elevation gradient (Fraaije  
551 et al., 2017), the greater occurrence of small-seed-mass species at middle elevation on  
552 naturally rejuvenated bars may be due to a greater range of flooding here than at other  
553 geomorphic surfaces, allowing the accumulation of small buoyant seeds near the average  
554 water line. Indeed, as compared to naturally rejuvenated bars, which are periodically subject  
555 to flood events, relict bars and reprofiled banks in bypassed sections are subject to flow  
556 regulation, which imply a fairly constant minimum flow most of the year. Additionally, areas  
557 that are flooded more frequently may be associated with greater environmental selection  
558 toward small seed mass. This possibility is evidenced by differences in mean seed mass  
559 values among naturally rejuvenated bars (mean  $\pm$ SD = 3.48  $\pm$ 2.88 mg), relict bars (4.15  $\pm$ 6.28  
560 mg) and reprofiled banks (6.42  $\pm$ 8.51 mg). Finally, mean SLA values decreased along the  
561 elevation gradient on only naturally rejuvenated bars. This result reveals a shift in plant  
562 growth rate strategy with elevation levels, from low to high resource conservation strategy,  
563 and highlights adaptation to drought stress (Chaves et al., 2003). Overall, our results confirm  
564 that naturally rejuvenated bars are more stressful environments than the two other geomorphic  
565 surfaces types, hosting distinct functional assemblages of plant species.

566 For diversity patterns, results showed that the richness and cover of hydrochorous species  
567 decreased less along the elevation gradient on newly reprofiled banks than on other  
568 geomorphic surfaces and were less abundant on naturally rejuvenated bars. Since clear links  
569 exist between seed abundance and fine sediment amount (Goodson et al., 2003), this result  
570 may show that hydrochorous species require a certain minimum proportion of fine sediments  
571 to successfully establish along river margins (e.g., Corenblit et al., 2016). Moreover, the cover

572 of alien species was higher on naturally rejuvenated bars and reprofiled banks than other  
573 geomorphic surfaces. For naturally rejuvenated bars, this result is mostly due to the  
574 overrepresentation of the ruderal species *Ambrosia artemisiifolia* (frequency of occurrence:  
575 81%); for reprofiled banks, this result is mostly due to the rapid colonization of newly  
576 available terrestrial habitats by *Symphytotrichum x salignum* (frequency of occurrence: 94%).  
577 Overall, we showed that the response of riparian plants to environmental gradients is mostly  
578 inconsistent among the three geomorphic surface types. This result is undoubtedly related to  
579 differences in environmental conditions and flow regimes between the Rhône River and its  
580 tributaries. This may confirm the alteration of the natural disturbance regimes of the Rhône  
581 River in terms of flow regulation and bedload supply and highlights their ecological  
582 consequences to the functionality of riparian habitats (e.g., Bejarano et al., 2017). Moreover,  
583 we showed that new terrestrial habitats resulting from restoration measures are in the same  
584 ecological trajectories of repeatedly cleared relict bars. Whereas the hydraulic efficiency of  
585 dike removal and bank reprofiling is not proven here (see Thorel et al. 2017), these findings  
586 suggest that their ecological added value is also questionable (e.g., Weber et al., 2009). In  
587 view of an effective ecological restoration of highly degraded river ecosystems (Molles, et al.,  
588 1998; Roni et al., 2002), we argue that (i) the minimum flow in bypassed sections of the  
589 Rhône River should vary more (see e.g., Hayes et al., 2018), (ii) bedload transport restoration  
590 should be a priority to allow for gravel bars that are more dynamic and (iii) newly reprofiled  
591 banks should better mimic landforms of natural river margins, by favoring low elevation  
592 surfaces and a high proportion of coarse sediments.

593

## 594 **5. CONCLUSION**

595 The need to disentangle interactions among natural and human-mediated environmental  
596 changes is important, and improved knowledge of these interactions could increase the

597 efficiency of conservation and restoration strategies (e.g., Dawson et al., 2017). Here, we  
598 showed that focusing on a single environmental gradient, such as the flood gradient, may lead  
599 to an incomplete understanding of the ecological processes that drives community assembly  
600 in riparian zones and that accounting for the influence that current human activity has on  
601 riparian biodiversity is fundamental to unraveling how environmental filtering acts on  
602 assembly processes. Specifically, we showed that biotic homogenization on river margins was  
603 clearly related to fine-grained alluviation processes. Since biotic homogenization alters  
604 ecosystem functioning and productivity and leads to the deterioration of ecosystem goods and  
605 services (Clavel et al., 2011), restoring the natural disturbance regimes should be a priority.  
606 Hence, on highly degraded rivers systems such as the Rhône River, the efficiency of local-  
607 scale restoration measures (e.g., bank reprofiling following dike removal) would benefit from  
608 a more global strategy of reactivation of bedload transport and supply at the reach and  
609 catchment scales (e.g., Rohde et al., 2005).

610

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847 Table 1. Top-ranked models predicting the mean and dispersion of ecological and  
848 morphological trait values and the richness and cover of species groups vs elevation and soil  
849 texture gradients as well as maintenance measures on repeatedly cleared relict bars along the  
850 Rhône River (France), as assessed with Akaike's information criterion corrected for small  
851 sample size (AICc). Number of estimated parameters including the intercept (k), AICc, AICc  
852 weight (*W*), marginal coefficient of determination for fixed effect ( $R^2$ ) and evidence ratio  
853 (ER), i.e., Akaike weight of the best model/Akaike weight of the second best model, are  
854 provided.

Measure	Variable	Top-ranked model	k	AICc	W	R <sup>2</sup>	ER
Ecological traits							
CWM:	Soil moisture	elevation + fine_sediments	6	257.5	0.225	0.506	1.02
	Light	elevation	5	138.5	0.199	0.022	0.00
	Nitrogen content	Null	4	138.0	0.258	0.000	0.00
FDis:	Soil moisture	fine_sediments	5	-44.3	0.443	0.166	0.99
	Light	elevation * fine_sediments + maintenance	8	-46.7	0.415	0.146	1.32
	Nitrogen content	fine_sediments * maintenance	7	-108.9	0.745	0.330	0.98
Morphological traits							
CWM:	SLA	Null	4	524.4	0.359	0.000	0.00
	Plant height	elevation * fine_sediments	7	24.5	0.530	0.212	0.99
	Seed mass	elevation	5	43.1	0.438	0.202	0.99
FDis:	SLA	elevation * maintenance + fine_sediments	8	-102.4	0.545	0.395	1.18
	Plant height	Null	4	165.2	0.238	0.000	0.00
	Seed mass	elevation + fine_sediments	6	64.9	0.238	0.059	2.95

Species groups

Richness:	Hydrochorous	elevation	5	403.3	0.279	0.517	0.94
	Annual	$\text{fine\_sediments} * \text{maintenance}$	7	691.6	0.520	0.389	0.99
	Alien	$\text{elevation} * \text{fine\_sediments} + \text{maintenance}$	8	478.8	0.354	0.303	1.02
Cover:	Hydrochorous	$\text{elevation} * \text{fine\_sediments}$	7	768.0	0.433	0.313	0.94
	Annual	$\text{fine\_sediments} * \text{maintenance}$	7	878.6	0.681	0.223	0.97
	Alien	$\text{elevation} * \text{maintenance}$	7	741.8	0.189	0.077	0.97

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856 Table 2. Average coefficients (Estimate ( $\pm$ SE)) and confidence intervals (95% CI) for fixed effects predicting the mean and dispersion of  
857 ecological and morphological trait values and the richness and cover of species groups vs elevation and soil texture gradients as well as  
858 maintenance measures on repeatedly cleared relict bars along the Rhône River (France). The 95% confidence intervals of coefficients in bold  
859 excluded 0.

Measure	Variable	elevation		fine_sediments		elevation:fine_sediments	
		Estimate ( $\pm$ SE)	(95% CI)	Estimate ( $\pm$ SE)	(95% CI)	Estimate ( $\pm$ SE)	(95% CI)
Ecological traits							
CWM:	Soil moisture	<b>-1.611 (<math>\pm</math>0.170)</b>	<b>(-1.945; -1.277)</b>	0.331 ( $\pm$ 0.202)	(-0.065; 0.726)	NA	NA
	Light	0.138 ( $\pm$ 0.089)	(-0.036; 0.312)	-0.068 ( $\pm$ 0.107)	(-0.277; 0.141)	NA	NA
	Nitrogen content	NA	NA	0.133 ( $\pm$ 0.099)	(-0.061; 0.328)	NA	NA
FDis:	Soil moisture	NA	NA	<b>-0.167 (<math>\pm</math>0.036)</b>	<b>(-0.238; -0.096)</b>	NA	NA
	Light	0.015 ( $\pm$ 0.041)	(-0.065; 0.094)	<b>-0.130 (<math>\pm</math>0.050)</b>	<b>(-0.227; -0.032)</b>	<b>0.212 (<math>\pm</math>0.067)</b>	<b>(0.080; 0.344)</b>
	Nitrogen content	NA	NA	<b>-0.097 (<math>\pm</math>0.028)</b>	<b>(-0.152; -0.042)</b>	NA	NA
Morphological traits							
CWM:	SLA	NA	NA	-0.419 ( $\pm$ 0.597)	(-1.590; 0.752)	NA	NA
	Height	<b>-0.188 (<math>\pm</math>0.056)</b>	<b>(-0.298; -0.078)</b>	<b>0.269 (<math>\pm</math>0.064)</b>	<b>(0.144; 0.394)</b>	<b>-0.201 (<math>\pm</math>0.092)</b>	<b>(-0.381; -0.021)</b>



	Seed	<b>0.295 (±0.054)</b>	<b>(0.189; 0.401)</b>	NA	NA	NA	NA
FDis:	SLA	<b>-0.152 (±0.030)</b>	<b>(-0.211; -0.093)</b>	<b>-0.087 (±0.035)</b>	<b>(-0.156; -0.018)</b>	NA	NA
	Height	-0.143 (±0.106)	(-0.352; 0.065)	0.113 (±0.117)	(-0.116; 0.342)	NA	NA
	Seed	0.135 (±0.072)	(-0.005; 0.276)	-0.142 (±0.079)	(-0.298; 0.013)	NA	NA
Species groups							
Richness:	Hydrochorous	<b>-1.686 (±0.185)</b>	<b>(-2.048; -1.324)</b>	-0.171 (±0.221)	(-0.603; 0.261)	NA	NA
	Annual	NA	NA	<b>-0.385 (±0.138)</b>	<b>(-0.655; -0.115)</b>	NA	NA
	Alien	-0.173 (±0.123)	(-0.415; 0.068)	-0.293 (±0.155)	(-0.596; 0.010)	<b>0.524 (±0.200)</b>	<b>(0.132; 0.915)</b>
Cover:	Hydrochorous	<b>-2.417 (±0.542)</b>	<b>(-3.479; -1.355)</b>	0.560 (±0.542)	(-0.503; 1.622)	<b>-2.731 (±1.115)</b>	<b>(-4.917; -0.545)</b>
	Annual	NA	NA	<b>-0.443 (±0.218)</b>	<b>(-0.870; -0.016)</b>	NA	NA
	Alien	-0.388 (±0.245)	(-0.868; 0.093)	0.323 (±0.279)	(-0.223; 0.869)	NA	NA

Measure	Variable	maintenance		elevation:maintenance		fine_sediments:maintenance	
		Estimate ( $\pm$ SE)	(95% CI)	Estimate ( $\pm$ SE)	(95% CI)	Estimate ( $\pm$ SE)	(95% CI)
Ecological traits							
CWM:	Soil moisture	-0.179 ( $\pm$ 0.234)	(-0.638; 0.280)	-0.353 ( $\pm$ 0.275)	(-0.892; 0.186)	NA	NA
	Light	0.111 ( $\pm$ 0.109)	(-0.103; 0.324)	NA	NA	NA	NA
	Nitrogen content	NA	NA	NA	NA	NA	NA
FDis:	Soil moisture	NA	NA	NA	NA	NA	NA
	Light	-0.085 ( $\pm$ 0.050)	(-0.184; 0.014)	NA	NA	NA	NA
	Nitrogen content	<b>0.103 (<math>\pm</math>0.037)</b>	<b>(0.030; 0.176)</b>	NA	NA	<b>0.242 (<math>\pm</math>0.057)</b>	<b>(0.130; 0.354)</b>
Morphological traits							
CWM:	SLA	NA	NA	NA	NA	NA	NA
	Height	NA	NA	NA	NA	NA	NA
	Seed	NA	NA	NA	NA	NA	NA
FDis:	SLA	0.050 ( $\pm$ 0.043)	(-0.034; 0.134)	<b>-0.138 (<math>\pm</math>0.055)</b>	<b>(-0.246; -0.030)</b>	NA	NA
	Height	NA	NA	NA	NA	NA	NA
	Seed	0.069 ( $\pm$ 0.109)	(-0.145; 0.283)	NA	NA	NA	NA

Species groups

Richness:	Hydrochorous	0.380 ( $\pm 0.273$ )	(-0.155; 0.915)	NA	NA	NA	NA
	Annual	<b>0.901 (<math>\pm 0.203</math>)</b>	<b>(0.503; 1.299)</b>	NA	NA	<b>0.722 (<math>\pm 0.289</math>)</b>	<b>(0.156; 1.288)</b>
	Alien	<b>0.633 (<math>\pm 0.176</math>)</b>	<b>(0.289; 0.978)</b>	NA	NA	0.516 ( $\pm 0.282$ )	(-0.037; 1.069)
Cover:	Hydrochorous	-0.710 ( $\pm 0.512$ )	(-1.714; 0.294)	NA	NA	NA	NA
	Annual	<b>0.843 (<math>\pm 0.257</math>)</b>	<b>(0.339; 1.347)</b>	NA	NA	<b>1.257 (<math>\pm 0.411</math>)</b>	<b>(0.451; 2.063)</b>
	Alien	0.529 ( $\pm 0.359$ )	(-0.175; 1.232)	-0.889 ( $\pm 0.459$ )	(-1.788; 0.010)	0.852 ( $\pm 0.496$ )	(-0.120; 1.825)

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862 Table 3. Top-ranked models predicting the mean and dispersion of ecological and  
863 morphological trait values and the richness and cover of species groups vs elevation and soil  
864 texture gradients as well as the type of geomorphic surface along the Rhône River and  
865 tributaries (France), as assessed with Akaike's information criterion corrected for small  
866 sample size (AICc). Number of estimated parameters including the intercept (k), AICc, AICc  
867 weight (*W*), marginal coefficient of determination for fixed effect ( $R^2$ ) and evidence ratio  
868 (ER), i.e., Akaike weight of the best model/Akaike weight of the second best model, are  
869 provided.

Measure	Variable	Top-ranked model	k	AICc	W	$R^2$	ER
Ecological traits							
CWM:	Soil moisture	elevation * type	9	468.2	0.654	0.560	1.89
	Light	elevation + type	7	230.1	0.372	0.143	1.94
	Nitrogen content	elevation * type	9	276.9	0.740	0.171	2.90
FDis:	Soil moisture	elevation * type + fine_sediments	10	-62.8	0.788	0.197	9.69
	Light	elevation * fine_sediments	7	-68.0	0.565	0.047	4.06
	Nitrogen content	fine_sediments	5	-181.3	0.431	0.050	1.83
Morphological traits							
CWM:	SLA	elevation * type + fine_sediments	10	980.2	0.570	0.112	1.34
	Plant height	elevation * fine_sediments + type	9	-33.7	0.541	0.175	2.44
	Seed mass	elevation * type	9	128.7	0.478	0.129	3.02
FDis:	SLA	elevation + fine_sediments	6	-180.8	0.395	0.247	1.76
	Plant height	Null	4	-358.2	0.259	0.000	1.54
	Seed mass	elevation + fine_sediments	6	134.9	0.305	0.037	1.81

Species groups

Richness:	Hydrochorous	elevation * type	9	748.7	0.608	0.544	1.55
	Annual	elevation * fine_sediments	7	1367.2	0.335	0.049	1.34
	Alien	Null	4	905.8	0.201	0.000	1.14
Cover:	Hydrochorous	elevation * type	9	1342.4	0.517	0.225	1.22
	Annual	elevation + fine_sediments	6	1801.3	0.180	0.026	1.51
	Alien	elevation * type	9	1542.2	0.293	0.126	1.21

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871 Table 4. Average coefficients (Estimate ( $\pm$ SE)) and confidence intervals (95% CI) for fixed effects predicting the mean and dispersion of  
872 ecological and morphological trait values and the richness and cover of species groups vs elevation and soil texture gradients as well as  
873 geomorphic surface types (Cleared = repeatedly cleared relict bars, Reprof = newly reprofiled banks, Natura = naturally rejuvenated bars) along  
874 the Rhône River and tributaries (France). The 95% confidence interval of coefficients in bold excluded 0.

Measure	Variable	elevation		fine_sediments		Elevation:fine_sediments	
		Estimate ( $\pm$ SE)	(95% CI)	Estimate ( $\pm$ SE)	(95% CI)	Estimate ( $\pm$ SE)	(95% CI)
Ecological traits							
CWM:	Soil moisture	<b>-1.817 (<math>\pm</math>0.174)</b>	<b>(-2.158; -1.477)</b>	0.130 ( $\pm$ 0.133)	(-0.131; 0.390)	NA	NA
	Light	<b>0.176 (<math>\pm</math>0.061)</b>	<b>(0.057; 0.295)</b>	-0.069 ( $\pm$ 0.072)	(-0.211; 0.073)	NA	NA
	Nitrogen content	0.016 ( $\pm$ 0.102)	(-0.184; 0.216)	NA	NA	NA	NA
FDis:	Soil moisture	-0.039 ( $\pm$ 0.048)	(-0.133; 0.055)	<b>-0.098 (<math>\pm</math>0.035)</b>	<b>(-0.167; -0.029)</b>	NA	NA
	Light	-0.002 ( $\pm$ 0.030)	(-0.061; 0.057)	-0.067 ( $\pm$ 0.035)	(-0.136; 0.002)	<b>0.167 (<math>\pm</math>0.058)</b>	<b>(0.053; 0.281)</b>
	Nitrogen content	0.022 ( $\pm$ 0.023)	(-0.023; 0.067)	<b>-0.075 (<math>\pm</math>0.025)</b>	<b>(-0.125; -0.026)</b>	NA	NA
Morphological traits							
CWM:	SLA	0.184 ( $\pm$ 0.630)	(-1.052; 1.419)	-0.805 ( $\pm$ 0.478)	(-1.743; 0.132)	NA	NA
	Height	-0.101 ( $\pm$ 0.065)	(-0.228; 0.027)	<b>0.138 (<math>\pm</math>0.039)</b>	<b>(0.062; 0.213)</b>	<b>-0.214 (<math>\pm</math>0.063)</b>	<b>(-0.337; -0.091)</b>

	Seed	<b>0.349</b> ( $\pm 0.070$ )	<b>(0.212; 0.486)</b>	NA	NA	NA	NA
FDis:	SLA	<b>-0.135</b> ( $\pm 0.023$ )	<b>(-0.179; -0.090)</b>	<b>-0.082</b> ( $\pm 0.027$ )	<b>(-0.135; -0.029)</b>	-0.045 ( $\pm 0.044$ )	(-0.132; 0.042)
	Height	<b>-0.460</b> ( $\pm 0.028$ )	<b>(-0.515; -0.406)</b>	<b>0.102</b> ( $\pm 0.008$ )	<b>(0.086; 0.119)</b>	NA	NA
	Seed	<b>0.110</b> ( $\pm 0.050$ )	<b>(0.013; 0.208)</b>	-0.112 ( $\pm 0.062$ )	(-0.233; 0.009)	0.056 ( $\pm 0.096$ )	(-0.132; 0.243)
Species groups							
Richness:	Hydrochorous	<b>-1.948</b> ( $\pm 0.215$ )	<b>(-2.370; -1.527)</b>	-0.172 ( $\pm 0.150$ )	(-0.466; 0.122)	NA	NA
	Annual	0.101 ( $\pm 0.086$ )	(-0.069; 0.270)	<b>-0.324</b> ( $\pm 0.126$ )	<b>(-0.571; -0.077)</b>	0.328 ( $\pm 0.174$ )	(-0.012; 0.669)
	Alien	<b>-0.091</b> ( $\pm 0.072$ )	<b>(-0.233; 0.050)</b>	-0.100 ( $\pm 0.097$ )	(-0.289; 0.089)	NA	NA
Cover:	Hydrochorous	<b>-3.037</b> ( $\pm 0.536$ )	<b>(-4.088; -1.987)</b>	0.460 ( $\pm 0.348$ )	(-0.223; 1.142)	NA	NA
	Annual	0.256 ( $\pm 0.151$ )	(-0.039; 0.551)	-0.330 ( $\pm 0.177$ )	(-0.676; 0.017)	0.150 ( $\pm 0.276$ )	(-0.391; 0.691)
	Alien	<b>-0.460</b> ( $\pm 0.028$ )	<b>(-0.515; -0.406)</b>	<b>0.102</b> ( $\pm 0.008$ )	<b>(0.086; 0.119)</b>	NA	NA

Measure	Variable	Cleared-Reprof		Cleared-Natura		Elevation:Cleared-Reprof	
		Estimate ( $\pm$ SE)	(95% CI)	Estimate ( $\pm$ SE)	(95% CI)	Estimate ( $\pm$ SE)	(95% CI)
Ecological traits							
CWM:	Soil moisture	-0.187 ( $\pm$ 0.208)	(-0.595; 0.221)	<b>-1.249 (<math>\pm</math>0.212)</b>	<b>(-1.664; -0.834)</b>	<b>0.111 (<math>\pm</math>0.231)</b>	<b>(0.658; 1.564)</b>
	Light	<b>0.269 (<math>\pm</math>0.122)</b>	<b>(0.030; 0.509)</b>	<b>0.300 (<math>\pm</math>0.124)</b>	<b>(0.057; 0.542)</b>	NA	NA
	Nitrogen content	0.195 ( $\pm$ 0.140)	(-0.079; 0.469)	<b>-0.285 (<math>\pm</math>0.140)</b>	<b>(-0.559; -0.011)</b>	-0.016 ( $\pm$ 0.140)	(-0.290; 0.258)
FDis:	Soil moisture	-0.084 ( $\pm$ 0.049)	(-0.180; 0.012)	-0.089 ( $\pm$ 0.051)	(-0.189; 0.011)	-0.054 ( $\pm$ 0.063)	(-0.177; 0.069)
	Light	NA	NA	NA	NA	NA	NA
	Nitrogen content	NA	NA	NA	NA	NA	NA
Morphological traits							
CWM:	SLA	-0.290 ( $\pm$ 1.348)	(-2.933; 2.352)	0.301 ( $\pm$ 1.366)	(-2.376; 2.979)	0.078 ( $\pm$ 0.806)	(-1.502; 1.658)
	Height	0.003 ( $\pm$ 0.046)	(-0.086; 0.093)	<b>-0.113 (<math>\pm</math>0.049)</b>	<b>(-0.209; -0.017)</b>	<b>0.144 (<math>\pm</math>0.068)</b>	<b>(0.010; 0.278)</b>
	Seed	-0.036 ( $\pm$ 0.121)	(-0.273; 0.201)	0.149 ( $\pm$ 0.121)	(-0.088; 0.386)	<b>-0.262 (<math>\pm</math>0.096)</b>	<b>(-0.450; -0.074)</b>
FDis:	SLA	0.025 ( $\pm$ 0.039)	(-0.051; 0.102)	-0.051 ( $\pm$ 0.040)	(-0.130; 0.027)	NA	NA
	Height	<b>0.929 (<math>\pm</math>0.017)</b>	<b>(0.895; 0.963)</b>	<b>0.713 (<math>\pm</math>0.024)</b>	<b>(0.665; 0.761)</b>	<b>0.462 (<math>\pm</math>0.021)</b>	<b>(0.420; 0.504)</b>
	Seed	0.069 ( $\pm$ 0.127)	(-0.180; 0.318)	-0.065 ( $\pm$ 0.138)	(-0.335; 0.206)	NA	NA



Species groups

Richness:	Hydrochorous	<b>0.543 (±0.233)</b>	<b>(0.087; 1.000)</b>	<b>-0.859 (±0.292)</b>	<b>(-1.432; -0.286)</b>	<b>0.154 (±0.279)</b>	<b>(0.607; 1.700)</b>
	Annual	NA	NA	NA	NA	NA	NA
	Alien	0.372 (±0.229)	(-0.078; 0.822)	0.155 (±0.230)	(-0.295; 0.605)	NA	NA
Cover:	Hydrochorous	0.081 (±0.552)	(-1.001; 1.163)	<b>-1.403 (±0.578)</b>	<b>(-2.536; -0.270)</b>	<b>2.304 (±0.631)</b>	<b>(1.069; 3.540)</b>
	Annual	0.609 (±0.372)	(-0.121; 1.338)	0.674 (±0.378)	(-0.066; 1.414)	NA	NA
	Alien	<b>0.929 (±0.017)</b>	<b>( 0.895; 0.963)</b>	<b>0.713 (±0.024)</b>	<b>(0.665; 0.761)</b>	<b>0.462 (±0.021)</b>	<b>(0.420; 0.504)</b>

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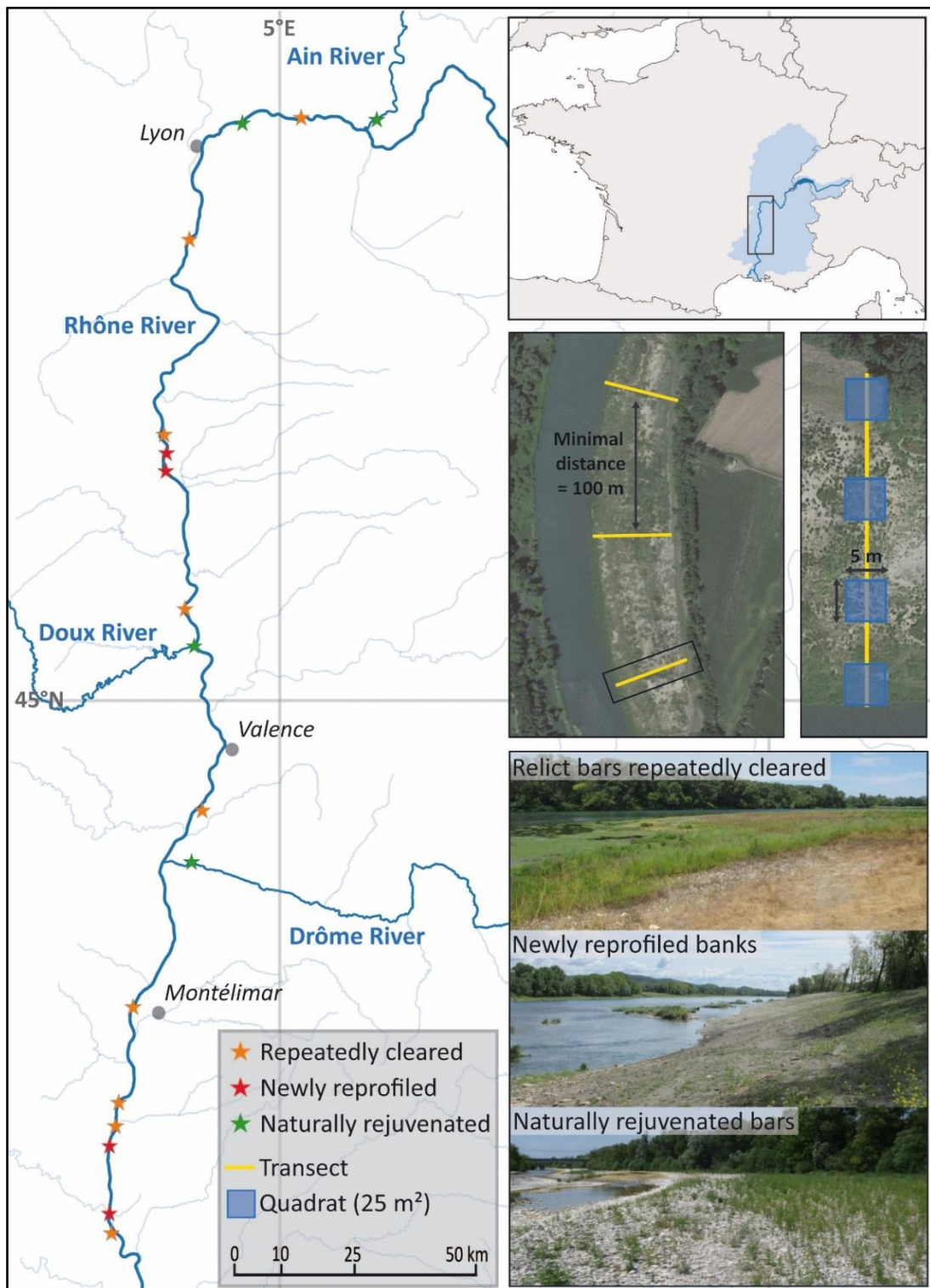
Measure	Variable	Elevation:Cleared-Natura		fine_sediments:Cleared-Reprof		fine_sediments:Cleared-Natura	
		Estimate ( $\pm$ SE)	(95% CI)	Estimate ( $\pm$ SE)	(95% CI)	Estimate ( $\pm$ SE)	(95% CI)
Ecological traits							
CWM:	Soil moisture	0.259 ( $\pm$ 0.326)	(-0.381; 0.898)	NA	NA	NA	NA
	Light	NA	NA	NA	NA	NA	NA
	Nitrogen content	<b>-0.808 (<math>\pm</math>0.201)</b>	<b>(-1.202; -0.414)</b>	NA	NA	NA	NA
FDis:	Soil moisture	<b>-0.312 (<math>\pm</math>0.087)</b>	<b>(-0.483; -0.141)</b>	NA	NA	NA	NA
	Light	NA	NA	NA	NA	NA	NA
	Nitrogen content	NA	NA	NA	NA	NA	NA
Morphological traits							
CWM:	SLA	<b>-5.287 (<math>\pm</math>1.130)</b>	<b>(-7.503; -3.072)</b>	NA	NA	NA	NA
	Height	<b>0.324 (<math>\pm</math>0.095)</b>	<b>(0.138; 0.509)</b>	NA	NA	NA	NA
	Seed	<b>-0.365 (<math>\pm</math>0.139)</b>	<b>(-0.637; -0.093)</b>	NA	NA	NA	NA
FDis:	SLA	NA	NA	NA	NA	NA	NA
	Height	<b>0.187 (<math>\pm</math>0.016)</b>	<b>(1.154; 1.219)</b>	NA	NA	NA	NA
	Seed	NA	NA	0.172 ( $\pm$ 0.144)	(-0.111; 0.454)	<b>-0.420 (<math>\pm</math>0.190)</b>	<b>(-0.793; -0.047)</b>

Species groups

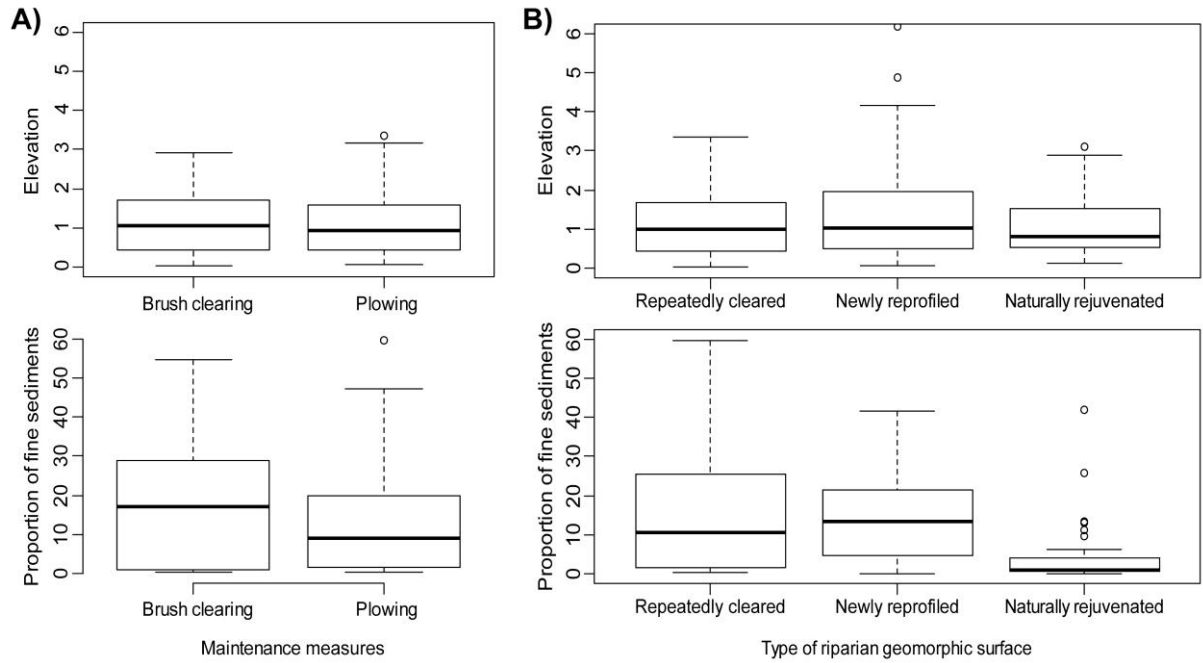
Richness:	Hydrochorous	-0.370 ( $\pm 0.559$ )	(-1.466; 0.726)	NA	NA	NA	NA
	Annual	NA	NA	NA	NA	NA	NA
	Alien	NA	NA	NA	NA	NA	NA
Cover:	Hydrochorous	-0.031 ( $\pm 0.987$ )	(-1.966; 1.904)	NA	NA	NA	NA
	Annual	NA	NA	NA	NA	NA	NA
	Alien	<b>1.187 (<math>\pm 0.016</math>)</b>	<b>(1.154; 1.219)</b>	NA	NA	NA	NA

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877 Figure 1. Location of the study area within the Rhône River watershed, distribution of  
 878 sampled geomorphic surfaces along the section of the Rhône River and the tributary rivers  
 879 studied (Ain, Drôme and Doux Rivers) and form of the sampling design used to survey plant  
 880 communities.

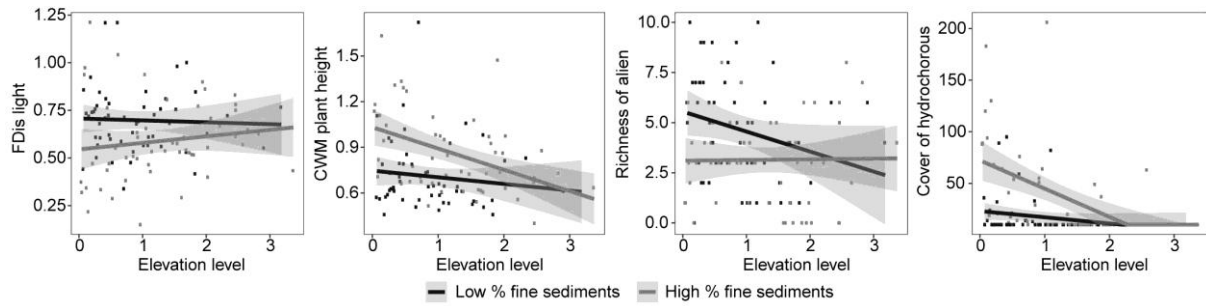


881 Figure 2. Variations in elevation and in the proportion of fine sediments in relation to A)  
 882 maintenance measures along repeatedly cleared relict bars of the Rhône riverbed (n quadrats  
 883 = 108) and B) the type of geomorphic surface (n quadrats = 204).

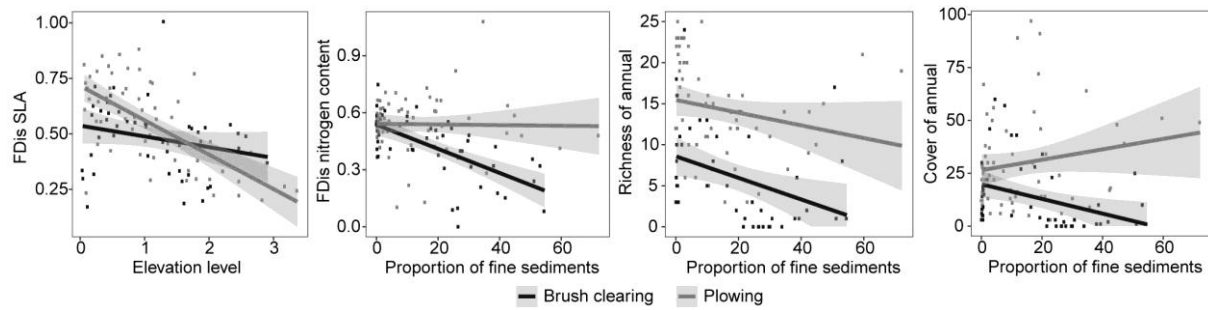


884

885 Figure 3. Interaction effect between elevation and soil texture on ecological and  
886 morphological traits and species groups on repeatedly cleared relict bars along the Rhône  
887 River (France). To provide representation, the proportion of fine sediments (continuous  
888 variable), has been divided into two equally sized groups.



889 Figure 4. Interaction effect between environmental gradients and maintenance measures on  
890 ecological and morphological traits and species groups on repeatedly cleared relict bars along  
891 the Rhône River (France).



892 Figure 5. Interaction effect between environmental gradients and the type of geomorphic  
 893 surface, i.e., A) repeatedly cleared relict bars vs newly reprofiled banks and B) repeatedly  
 894 cleared relict bars vs naturally rejuvenated bars, on ecological and morphological traits and  
 895 species groups along the Rhône River and tributaries (France).

