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1 **Fine-grained sediment deposition alters the response of plant CSR strategies on the gravel bars of a highly**
2 **regulated river**

3

4 Running head: Sedimentation changes CSR strategies

5

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15 **ABSTRACT**

16 **Aims:** In riverine ecosystems, variations in disturbance and stress intensities along the flood gradient shape the
17 community structure. However, human modifications to the flood regime may change the magnitude of
18 disturbance and stress, leading to different species distribution patterns along environmental gradients. We
19 aimed to study the effects of local- and broad-scale environmental gradients on riparian plant CSR strategies
20 along a highly regulated river.

21 **Location:** Rhône River, France.

22 **Methods:** We assessed how changes in elevation, fine sediment content and annual temperature influenced
23 CSR strategies of riparian communities, by studying variations in CWM and FDis, on gravel bars along a 250 km
24 north-south river corridor.

25 **Results:** Species with contrasting ecological strategies co-occurred less on gravel bars subject to fine sediment
26 deposition, leading to patterns of biotic homogenization along the flood gradients. Furthermore, a shift in CSR
27 strategies from ruderal to stress-tolerant communities was highlighted along the elevation gradient on the bars
28 with low proportions of fine sediments and from stress-tolerant to ruderal communities along the elevation
29 gradient on the bars with high proportions of fine sediments. Regarding the climatic gradient, the ruderal
30 dimension of communities increased with the average temperature. Also, the stress-tolerant dimension of
31 communities diverged between the north and south gravel bars when the proportion of fine sediments was
32 low and converged when the proportion of fine sediments was high.

33 **Conclusions:** Overbank fine sedimentation alleviates the intensity of stress along not only the elevation
34 gradient but also the climatic gradient. By homogenizing the functional composition of communities, this
35 process may have detrimental consequences for riparian plants diversity, especially the ruderal pioneer
36 communities in the tidal zone. In regulated river systems, restoration measures should therefore
37 comprehensively integrate an increase in the intensity of (i) disturbance through the reactivation of bedload
38 supply and transport and (ii) stress through increased flow dynamics.

39

40 **Keywords:** community structure, ecological strategies, environmental gradients, flood gradient, functional
41 ecology, Grime's CSR theory, overbank fine sedimentation, riparian ecology

42 INTRODUCTION

43 Grime's CSR theory is perhaps one of the most influential niche-based theories of plant community assembly
44 and vegetation succession (Li & Shipley 2017). This theory proposes to both functionally classify plants and
45 predict changes in the community structure along environmental gradients by focusing on only three
46 dimensions of a ternary ordination plot describing the responses of species to disturbance (i.e., partial or total
47 destruction of biomass) and stress (i.e., external constraints that restrict biomass production) intensities (Grime
48 1977). Recent advances in functional ecology have shown that the use of three representative leaf traits (i.e.,
49 leaf area, leaf dry matter content and specific leaf area) can be used to determine the ecological strategies of
50 plant species in a wide range of ecosystems (Pierce et al. 2017). Through the linkages between leaf traits and
51 CSR functional strategies applied in a unified framework, it now appears possible to quantitatively compare the
52 strategy-environment relationships of vascular plants. Furthermore, by using the ternary coordinates of each
53 species, it become possible to compute a community-wide average strategy (e.g., Li & Shipley 2017) and thus
54 avoid the use of large categories of plant functional types (Van Bodegom et al. 2012). Overall, this approach
55 gives an empirical link between CSR theory and the functional structure of vegetation, making it possible to
56 compare the strategies of plant communities along environmental gradients and/or in response to human-
57 induced changes (e.g., Caccianiga et al. 2006; Li & Shipley 2017).

58 Riparian zones are transitional areas at the interface between freshwater and terrestrial ecosystems where
59 sharp environmental gradients shape the community structure (Naiman & Decamps 1997). Due to the
60 variations in disturbance (i.e., flood regime) and stress (i.e., soil moisture and nutriments) intensities from the
61 lower to the upper parts of banks, these dynamic ecosystems encompass a wide variety of habitat
62 geomorphology, which induces niche differentiation and a shift in trait values (Blom 1999; Lytle & Poff 2004;
63 Steiger et al. 2005). As a result, predictable successional pathways are usually reported along elevation
64 gradients from ruderal to competitor life strategies (Kyle & Leishman 2009; McCoy-Sulentic et al. 2017).

65 However, the alteration of the flow and sediment regimes of most rivers worldwide has led to changes in the
66 response of riparian plant species guilds to the flood gradient (Bejarano et al. 2018; Aguiar et al. 2018). Indeed,
67 flow regulation induces a decrease in the intensity and magnitude of the inundation regime (Poff et al. 1997;
68 Poff et al. 2007), which limits the destruction of plant biomass by scouring and thus favors vegetation
69 encroachment by drought-adapted species (Merritt & Poff 2010; González et al. 2010; Nadal-Sala et al. 2017).
70 Moreover, a low level of disturbance may prevent remobilization of coarse-grained alluvial sediments but

71 promote the deposition of the solid suspended load by gravitation, i.e. fine-grained alluvial sediments (Wilkes
72 et al. 2019). Accretion of fine sediments increases the water-holding capacity and nutrient availability (Steiger
73 & Gurnell 2003; Asaeda & Sanjaya 2017), thereby reducing the intensity of stress along local environmental
74 gradients and promoting an increase in net primary production of vegetation (Asaeda & Rashid 2012).

75 Beyond the direct influence of human activity on local-scale environmental gradients, climate change has been
76 emphasized as a major threat to riparian communities (Perry et al. 2012; Garssen et al. 2017). Temperature
77 increase are expected to increase the intensity of stress along flood gradients, inducing growth reductions and
78 dieback of riparian vegetation (Ström et al. 2012; Rivaes et al. 2013; Stella, Riddle, et al. 2013). Moreover,
79 changes in precipitation may increase the magnitude and frequency of flood events, amplifying the alteration
80 of the disturbance regime in rivers, eventually leading to shifts in plant species composition (Garssen et al.
81 2015; Garssen et al. 2017). These modifications to disturbance and stress intensities over a large scale may
82 further interact with local-scale gradients and exacerbate the related environmental changes, for example, by
83 increasing the intensity of stress along the elevation gradient in riparian zones located in warm climates. As
84 such, it has been shown that riparian plant communities respond consistently to local-scale hydrologic changes
85 and broad-scale climatic changes (Butterfield et al. 2018). This finding suggests that environmental changes
86 related to human activity at different scales may have cumulative effects on the structure and dynamics of
87 plant communities. However, despite the importance of understanding plant responses to human-induced
88 changes in shaping future vegetation, to the best of our knowledge, no empirical studies have yet investigated
89 the relationship between plant CSR strategies and multiple environmental gradients in riparian zones.

90 We aimed to study the effects of elevation and fine-grained deposition gradients on riparian plant CSR
91 strategies along the highly regulated Rhône River. By focusing on gravel bars that are more or less subjected to
92 overbank fine sedimentation along a 250 km north-south river corridor, we further aimed to understand
93 whether the response of riparian plant strategies to local environmental gradients is mediated by a broad
94 climatic gradient. Specifically, we tested whether and how the community-weighted mean values (C_{CWM} , S_{CWM}
95 and R_{CWM}) and the functional dispersion values (C_{FDIS} , S_{FDIS} and R_{FDIS}) were influenced by elevation level, the
96 proportion of fine sediments and the mean annual temperature. The mean value (i.e., average CSR values of all
97 species co-occurring in the community) expresses the dominant value of CSR strategy along environmental
98 gradients, while the dispersion value (i.e., the range of CSR values exhibited by species in the community)
99 expresses the extent of CSR differences among co-occurring species. Analytical strategies that combine both

100 measures have been showed to describe two complementary aspects of the relationship between community
101 structure and ecosystem functioning: (i) shifts in trait values due to environmental selection and (ii) patterns of
102 trait convergence or divergence due to niche differentiation (Ricotta & Moretti 2011; de Bello et al. 2013).

103 Within this framework, we explored the following three hypotheses based on Grime's CSR theory:

- 104 (1) Competitors increase from low to high proportions of subsoil fine sediments at middle to high
105 elevations along the northern gravel bars in the Rhône corridor (i.e., low disturbance with low stress);
- 106 (2) Stress-tolerators increase from high to low proportions of subsoil fine sediments at middle to high
107 elevations along the southern gravel bars of the Rhône corridor (i.e., low disturbance with high stress);
- 108 (3) Ruderals increase from high to low elevations, regardless of the proportion of subsoil fine sediments
109 and the mean annual temperature (i.e., high disturbance with low stress).

110

111 **MATERIALS & METHODS**

112 **Study area and experimental design**

113 The study was carried out along the Rhône River (total length = 810 km, catchment area = 96,500 km², mean
114 annual discharge = 1,700 m³/s) in its middle reach (Figure 1). This area is characterized by a temperate climate
115 with mean annual temperatures and precipitation of 13.6°C and 755 mm in the southern part and 11.6°C and
116 815 mm in the northern part of the study area. Two historical development phases have greatly altered the
117 functioning of this large river: (i) during the 19th century, a rectification phase, characterized by the building of
118 a vast system of longitudinal submersible and transversal dikes in the main channel, was carried out to
119 facilitate navigation; (ii) in the second half of the 20th century, a derivation phase, characterized by the
120 construction of a series of lateral canals, running parallel to the natural Rhône River channel, was carried out to
121 produce hydropower and facilitate irrigation and navigation (for details see, Bravard and Gaydou 2015). These
122 two development phases induced significant impacts in the bypassed sections (i.e., part of the historical Rhône
123 River channel), including changes to the hydrological regime (i.e., a reduction in the frequency and magnitude
124 of the peak flows, Vázquez-Tarrío et al. 2019), channel dewatering, incision and lateral stabilization. These
125 reaches also underwent a bedload supply interruption, with gravel winnowing and bed armoring; thus,
126 present-day bedload transport is limited to fine-grained sediments (Vázquez-Tarrío et al. 2019). Currently, the
127 bypassed sections are characterized by a minimum flow that is observed most of the year until the hydropower
128 plant capacity is reached.

129 In the summers of 2017 and 2018, we sampled 15 gravel bars in 8 different bypassed sections of the Rhône
130 River, along an approximately 250 km north-south reach (Figure 1). The studied gravel bars are fixed in the
131 bypassed sections of the Rhône riverbed, i.e., coarse sediments are no longer remobilized during flood events
132 and are subject to fine-grained overbank sedimentation and colonization by trees. To prevent encroachment of
133 these surfaces by trees and shrubs and the associated channel narrowing, maintenance measures are
134 implemented by river managers to scrap woody vegetation by either brush clearing (n = 7, in the north) or
135 plowing (n = 8, in the south).

136 **Vegetation data**

137 On each gravel bar, the vegetation was surveyed along three transects spaced at a distance of approximately
138 100 m from each other (Figure 1). Transects were positioned perpendicular to the river in areas with clear
139 elevation gradients relative to the water surface (means \pm SD = 1.16 \pm 0.85 m; range = 0.04-3.84 m). Transect
140 length varied from 30 m to 105 m, depending on the width of the gravel bar. The gradients started at the water
141 line and ended before the alluvial floodplain, which was mostly occupied by riparian forest. Along each
142 transect, four 5 x 5 m quadrats (25 m²) were positioned for a total of 12 quadrats per gravel bar. The quadrats
143 were positioned in visually homogenous areas while avoiding the aquatic parts of the river margin. Within each
144 quadrat (n = 180), all vascular plants were surveyed following Braun-Blanquet abundance/dominance
145 methodology. Because gravel bars along the Rhône River were repeatedly cleared, tree and shrub layers were
146 systematically absent and vegetation surveys were conducted by considering the herbaceous layer only. To
147 characterize the entire plant community and account for plant phenology, two complete surveys were
148 conducted each year (June and July), and to limit observer biases, all surveys were performed by the first
149 author (PJ).

150 **Riparian plant ecological strategies**

151 For each plant species, the ternary coordinates, i.e., C-dimension, S-dimension and R-dimension values within
152 the triangular CSR ordination, were extracted from the list of plant species (n = 3 068) available in Pierce *et al.*
153 (2017, Appendix S1). The ternary coordinates were originally calculated using a global CSR analysis tool that
154 necessitates the use of only three representative and easily measured leaf traits: leaf area, leaf dry matter
155 content and specific leaf area (for details see, Pierce et al. 2017). Among the 233 plant species assessed in our
156 study, the ternary coordinates of 179 species were documented in Pierce *et al.* (2017). For the missing values,
157 data were either completed by using ecological information on closely related species, i.e., the same genus (n

158 species = 38), or discarded (n species = 16). Most of the discarded species were rare (i.e., 11 species were
159 singletons) and/or exhibited low vegetation cover. Within each quadrat, we then computed (i) the community-
160 weighted means (CWMs) of the CSR values (hereafter, C_{CWM} , S_{CWM} , R_{CWM}) and (ii) the functional dispersion
161 (FDis) of the CSR values (hereafter, C_{FDis} , S_{FDis} , R_{FDis}) (FD package, Laliberté et al. 2014). CWM is defined as the
162 mean of the CSR values weighted by the relative cover of each species bearing each value (Lavorel et al. 2008).
163 FDis is defined as the mean distance of individual species to the weighted centroid of all species in the
164 assemblage (Laliberté & Legendre 2010).

165 **Environmental gradients**

166 The elevation and fine-grained deposition gradients were assessed in the field at the center of each quadrat.
167 The relative elevation above the water line was characterized using topographical surveys. Topographical
168 measurements were conducted using a laser rangefinder (TruPulse 200X) positioned on a tripod at a constant
169 height of 1.20 m and a target at a height of 2 m. The horizontal distance between the tripod and the target was
170 measured between the water line at the beginning of each transect and the center of four successive quadrats.
171 The fine-grained deposition was derived from two soil core samples (30-cm depth) collected in two
172 representative areas within each quadrat and pooled together. Each composite soil sample was then dried,
173 weighed and sieved in the laboratory to estimate the proportion of fine sediments (i.e., <250- μ m mesh). The
174 temperature gradient was derived from the WorldClim climatic model (Hijmans et al. 2005). The mean annual
175 temperature was averaged for each plot over the period 1970-2000 and adjusted for the effect of altitude
176 following Zimmermann and Kienast (1999).

177 **Statistical analysis**

178 The continuous independent variables (Appendix S2) were the elevation difference (denoted "Elevation" in
179 tables and figures), the proportion of fine sediments (denoted "Sediments") and the mean annual temperature
180 (denoted "Temperature"). Because the independent variables were measured on different units and because
181 we were interested in interpreting the main effects of the continuous variables in the presence of interactions,
182 the elevation and temperature variables were scaled (Schielzeth 2010), and the sediment variable (i.e.,
183 proportional data) was logit transformed prior to the analyses. The dependent variables were the community
184 mean values (i.e., CWM) and the functional dispersion values (i.e., FDis) of the plant ecological strategies in
185 each quadrat.

186 We used a modeling approach to determine whether elevation and fine-grained deposition gradients shape
187 riparian plant strategies and to what extent the changes in temperature induced changes in the responses of
188 plants to the local environmental gradients along the Rhône River. We considered a set of 13 *a priori* models,
189 testing the main and interaction effects between elevation, sediments and temperature variables, plus a null
190 model. Because the quadrats located on the same gravel bar may have a high chance of sharing similar plant
191 species, we used linear mixed models (LMMs) in which “transect” was nested in “gravel bar” ($n = 15$) and
192 included as a random effects (lme4 package, Bates et al. 2015). Also, because maintenance measures on
193 gravels bars is confounded with the temperature variable, i.e., bars in the north were maintained by brush
194 clearing while bars in the south were maintained by plowing, we included “management” factor as a covariate
195 in all the *a priori* models. We then fitted normal LMMs for C_{CWM} , S_{CWM} , R_{CWM} and C_{FDis} , S_{FDis} , R_{FDis} dependent
196 variables. In all candidate models, the variance inflation factor among elevation, sediments and temperature
197 variables was below three, indicating a lack of collinearity. The variance explained by the models was estimated
198 using the marginal coefficient of determination for the fixed effect parameters alone (Nakagawa & Schielzeth
199 2013). To identify the most parsimonious regression model, we used Akaike’s information criterion corrected
200 for small sample sizes (Burnham & Anderson 2002). Moreover, we used model averaging to estimate the
201 parameters and associated unconditional standard errors based on the subset of the top-ranking models for
202 which the sum of the AICc weights reached ≥ 0.95 (MuMIn package, Barton 2015).

203 Analyses were performed with R version 3.5.1 (R Core Team 2019).

204

205 **RESULTS**

206 Overall, 233 plant species (mean \pm SD = 25.3 ± 10.7) were recorded in the 180 quadrats along the Rhône River:
207 32 species (3.5 ± 1.9) were competitors (i.e., species C-dimensions $> 50\%$), 39 species (4.1 ± 2.4) were stress-
208 tolerators (i.e., species S-dimensions $> 50\%$), 84 species (6.8 ± 4.2) were ruderals (i.e., species R-dimensions $>$
209 50%), 62 species were not related to a dominant strategies (10.5 ± 4.5), while 17 species were discarded
210 (Appendix S1).

211 **Influence of environmental gradients on the community-weighted mean values of CSR plant strategies**

212 For the CWM values, C_{CWM} was best predicted by the “Sediments” model only, S_{CWM} was best predicted by the
213 interaction model “Elevation + Temperature*Sediments” while R_{CWM} was best predicted by the interaction
214 model “Temperature + Elevation*Sediments”. The goodness of fit of these models ranged from 4.1 % to 13.2 %

215 (Table 1), and model selection uncertainty remained since none of the top-ranking models showed strong
216 support to explain the community mean values. We therefore used model averaging to draw inferences about
217 the variables influencing C_{CWM} ($N_{models} = 11$), S_{CWM} ($N_{models} = 11$) and R_{CWM} ($N_{models} = 10$) (i.e., based on sum of the
218 AICc weights, see Appendix 3). The estimated parameters and related confidence intervals (Table 2) showed
219 that an increase in temperature induced a significant increase in R_{CWM} values. The interaction between
220 elevation and sediments significantly influenced the values of S_{CWM} and R_{CWM} , while the interaction between
221 sediments and temperature significantly influenced the value of S_{CWM} . A graphical interpretation revealed that
222 S_{CWM} increased with elevation when the proportion of fine sediments was low but decreased when the
223 proportion of fine sediments was high; the value of R_{CWM} decreased with elevation when the proportion of fine
224 sediments was low but increased when the proportion of fine sediments was high (Figure 2). Additionally, S_{CWM}
225 increased with the proportion of fine sediments when the temperature was high but decreased when the
226 temperature was low (Figure 4).

227 **Influence of environmental gradients on the functional dispersion values of CSR plant strategies**

228 For the FDis values, C_{FDis} was best predicted by the “Sediments” model only, S_{FDis} was best predicted by the
229 interaction model “Elevation + Temperature*Sediments” while R_{FDis} was best predicted by the interaction
230 model “Elevation*Sediments”. The goodness of fit of these models ranged from 10.4 % to 14.8 % (Table 1), and
231 model selection uncertainty remained since none of the top-ranking models showed strong support to explain
232 the functional dispersion values. We therefore used model averaging to draw inferences about the variables
233 influencing C_{FDis} ($N_{models} = 8$), S_{FDis} ($N_{models} = 6$) and R_{FDis} ($N_{models} = 4$) (see Appendix 3). The estimated parameters
234 and related confidence intervals (Table 2) showed that an increase in the proportion of fine sediments induced
235 a significant decrease in C_{FDis} values. The interaction between elevation and sediments significantly influenced
236 the values of S_{FDis} and R_{FDis} , the interaction between elevation and temperature significantly influenced the
237 value of R_{FDis} , while the interaction between sediments and temperature significantly influenced the value of
238 S_{FDis} . A graphical interpretation revealed that S_{FDis} and R_{FDis} values increased with elevation when the proportion
239 of fine sediments was high but decreased when the proportion of fine sediments was low (Figure 2).
240 Additionally, R_{FDis} increased with elevation when the temperature was high but slightly decreased when the
241 temperature was low (Figure 3), while S_{FDis} decreased more rapidly with the proportion of fine sediments when
242 the temperature was low (Figure 4).

243

244 **DISCUSSION**

245 We determined whether riparian plant strategies responded to both local- and broad-scale environmental
246 gradients in a large, regulated river, using the quantitative values of the CSR triangle dimensions (Pierce et al.
247 2017). We showed that elevation differences and the proportion of fine sediments had non-independent
248 effects on the plant strategies and specifically that fine-grained sediment deposition induced shifts in the
249 responses of stress-tolerant and ruderal communities to the flood gradient on the gravel bars. At a broad scale,
250 variations in climatic conditions along the studied north-south reach induced an increase in the ruderal
251 dimension of the plant communities along the southern gravel bars. However, overbank sedimentation
252 mitigated the effect of the climatic gradient by promoting a less stressful environment (i.e., increasing water-
253 holding capacity and nutrient availability), thus homogenizing the functional composition of the plant
254 communities on bars with high proportions of fine sediments. Overall, this shows that fine-grained sediment
255 deposition alleviates the intensity of stress along not only local flood gradients but also broad climatic
256 gradients, with potential detrimental consequences for riparian biodiversity conservation.

257 **Fine-grained sediment deposition induces a shift in plant strategies along the flood gradient**

258 Contrary to the hypothesis, CSR plant strategies were not structured in a predictable manner at the local scale.
259 Indeed, the dispersion values for stress-tolerant species increased at low elevations (i.e., co-occurring species
260 in low elevation communities exhibited a larger range of S-values), while the mean and dispersion values for
261 ruderal species increased at high elevations (i.e., co-occurring species in high elevation communities exhibited
262 a larger range of R-values and the average R value was higher). Given that CSR theory predicts that severely
263 disturbed environments favor rapidly growing plant species that are capable of rapidly producing seeds (Grime
264 1977), we expected to find the opposite pattern. However, our results also showed that plant strategies were
265 significantly influenced by fine-grained deposition, i.e. that an increase in the proportion of fine sediments
266 induced decreases in the co-occurrence of competitive, stress-tolerant and ruderal species (i.e. in the
267 dispersion values, Table 2). This means that species with contrasting ecological strategies co-occurred less on
268 bars subject to overbank fine sedimentation and thus that this process leads to patterns of biotic
269 homogenization along local environmental gradients (Olden & Rooney 2006). Specifically, our results
270 highlighted that plant strategies were significantly influenced by the interaction between the fine-grained
271 deposition and elevation level gradients. Indeed, by considering the differences in proportions of fine
272 sediments, we highlighted that the mean and dispersion values for stress-tolerant and ruderal plant species

273 changed in opposite direction along the flood gradient. This shift in CSR plant strategies from low to high
274 elevation levels revealed a restructuring of the local communities in gravel bars subject to fine-grained
275 sediment deposition. Thus, in highly disturbed environments (i.e., at low elevation), gravel bars supported
276 riparian plant communities dominated by ruderal species, while allowing for broader co-occurrence of species
277 with different stress-tolerant and ruderal strategies (i.e., niche differentiation was high). Reversely, on gravel
278 bars where large deposits of fine sediment occur, riparian plant communities at low elevation were dominated
279 by stress-tolerant species and the co-occurrence of species with different stress-tolerant and ruderal strategies
280 was low. Overall, these results demonstrated that, at least along the regulated Rhône River, the intensities of
281 disturbance and stress may significantly vary among gravel bars according to overbank sedimentation, which
282 will strongly change the strategy-environment relationships of the riparian plant communities.

283 The alterations to flow and sediment regimes by human activities have been shown to substantially degrade
284 the functionality of river ecosystems. Flow regulation by dams is well known to directly reduce the downstream
285 intensity of disturbance, lowering the flood peak and bedload transport (Nilsson & Berggren 2000; Poff et al.
286 2007) and limiting the destruction of plant biomass by coarse bed scour and burial disturbances (e.g., Polzin &
287 Rood 2006; Kui & Stella 2016). Moreover, a fairly constant minimum flow, as is the case in the bypassed
288 sections of the Rhône River, provides longer periods of growth for plant species (Poff et al. 2007).

289 Simultaneously, a low level of disturbance and an increase in vegetation roughness following encroachment
290 favor the deposition of fine sediments (Wilkes et al. 2019), which indirectly reduces the intensity of stress by
291 increasing the soil water-holding capacity and nutrient availability (Steiger & Gurnell 2003; Asaeda & Sanjaya
292 2017). Altogether, these changes promote environmental homogenization along the flood gradient, which
293 fosters the spread of competitive and stress-tolerant communities made up of perennial species and including
294 few dominant clonal species at low elevations. In turn, perennial vegetation traps and stabilizes fine sediments
295 (Corenblit et al. 2009), further lowering the intensity of stress. Additionally, clonal species such as *Phragmites*
296 *australis* and *Phalaris arundinacea* are known to impede the development of other species by shading and
297 inhibiting their germination through the production of a thick litter layer (Craft 2016), which may lead to
298 changes in biotic interactions at the expense of ruderal species. Thus, despite numerous studies have shown
299 that flow regulation benefits species that allocate resources to vegetative growth or the maintenance of
300 resources, at the expense of species that allocate resources to propagules (e.g., Merritt & Poff 2010; González
301 et al. 2010; Tonkin et al. 2018; Aguiar et al. 2018), we demonstrated here that this effect was primarily driven

302 by fine-grained sediment deposition. We therefore inferred that the shift in CSR strategies we documented on
303 the Rhône River is due to a decrease in the intensity of disturbances, in relation to flow regulation and
304 diversion (Vázquez-Tarrío et al. 2019), and a decrease in the intensity of stress, in relation to the deposition of
305 fine sediments, which deeply altered the successional pathways usually observed in riparian zones.

306 Nevertheless, it must be kept in mind that the studied riparian communities were moderately explained by the
307 models (i.e., the goodness of fit was always lower than 15 %). This may indicate not only that other important
308 factors were not accounted for in the analysis but also that environmental homogenization may promote a
309 greater stochastic distribution of species along degraded riparian zones.

310 **Fine-grained sediment deposition mitigates the effect of the climatic gradient**

311 The climatic gradient directly influenced CSR plant strategies. Indeed, along the north-south Rhône River
312 corridor, we found that an increase in temperature induced an increase in the mean values for ruderal plant
313 species. Given that ruderals are predominantly fast-growing species with an annual life cycle (Grime 1977;
314 Pierce et al. 2017), this result suggests that a warmer climate benefits species better adapted to exploit
315 environments that become intermittently favorable. Accordingly, in semiarid conditions, it has been shown
316 that the richness and cover of annual species increased at drier sites (Stromberg et al. 2009; Reynolds &
317 Shafroth 2017). This may indicate the vulnerability of riparian communities to climate changes (Perry et al.
318 2012) through direct changes in temperature and precipitation and indirect modifications to streamflow, i.e.,
319 by increasing low-flow events and peak flow magnitudes (Poff et al. 1997). However, related changes in the
320 streamflow components are expected to have greater consequences for riparian vegetation in arid and
321 semiarid areas (Garssen et al. 2014), especially in ephemeral streams (Friedman & Lee 2002; Stromberg et al.
322 2017). Indeed, along the regulated Rhône River, a fairly constant minimum flow is ensured all year round. This
323 may temper the effects of climatic variations and explain the absence of an interaction effect between
324 elevation and temperature on the mean value of ruderal communities. Instead, we found that the dispersion
325 values for ruderal species was influenced by the interaction between temperature and elevation, specifically
326 that the co-occurrence of species with different ruderal strategies increases along the elevation gradient with
327 increasing temperatures but tended to decrease with decreasing temperatures. This means that riparian
328 communities on the southern gravel bars harbor a greater diversity of plant strategies, i.e., including both
329 species with a primary ruderal strategy and species with a secondary ruderal strategy. Given that riparian plant
330 species richness is known to increase with drainage size (Kuglerová et al. 2015), we inferred that the interaction

331 effect reported herein simply reflects the arrival of new species that progressively increase the species pool
332 with downstream position of gravel bars in the river network. This reveals the difficulty to disentangle the
333 climatic gradient from the longitudinal gradient in riverine ecosystems.

334 In addition to the ruderal dimension of plant communities, we found that both the mean and dispersion values
335 of stress-tolerant plant species were significantly influenced by the interaction between temperature and the
336 proportion of fine sediments. Specifically, our results show that the dominant value of the stress-tolerant
337 dimension of plant communities diverged between the north and south gravel bars when the proportion of fine
338 sediments was low and tended to converge when the proportion of fine sediments was high. Interestingly,
339 although not significant, the same pattern was observed for the dominant value of the ruderal dimension. This
340 may indicate that in highly regulated rivers, fine-grained sediment deposition mitigates the effect of the
341 climatic gradient, e.g., by promoting less stressful environmental conditions (Steiger & Gurnell 2003; Asaeda &
342 Rashid 2012; Asaeda & Sanjaya 2017). Moreover, we found that the co-occurrence of species with different
343 stress-tolerant strategies decreased with increasing proportion of fine sediments, and that this effect was more
344 pronounced along the northern gravel bars. This shows that fine-grained sediment deposition increases the
345 functional similarity of plant communities across gravel bars, which reduces the species pool. In a context of
346 widespread degradation of riparian zones, overbank fine sedimentation may thus further reduce the
347 adaptability of riparian communities by inducing a selection in plant strategies toward a limited range of values.
348 This is especially true in temperate climates where species are less well-adapted to high levels of stress (e.g.
349 Singer et al. 2013; Stella, Rodríguez-González, et al. 2013) and where this absence of adaptation may render
350 riparian ecosystems highly vulnerable to climate change impacts (Capon et al. 2013). Nevertheless, given that
351 the climatic gradient in this study is unreplicated, caution must be exerted when drawing conclusions about the
352 drivers behind the patterns observed, as they may be confounded with the upstream-downstream axis of the
353 river.

354

355 **CONCLUSION**

356 In a recent review, Solari *et al.* (2016) noted the need to better account for soil properties in models that
357 incorporate the processes that relate riparian vegetation to hydromorphology. By quantitatively comparing the
358 strategy-environment relationships of riparian plants and by considering the individual and interactive effects
359 of elevation and fine-grained deposition along a north-south river corridor depicting a climatic gradient, we

360 were able to better explain the processes that shape the distribution of CSR plant strategies on gravel bars. Our
361 results thus confirm the importance of considering processes that are both directly (i.e., disturbance-related
362 processes) and indirectly (i.e., stress-related processes) linked to the flow regime to better understand the
363 structure and dynamic of riparian communities. More generally, our results lend weight to the idea that fine-
364 grained sediment deposition is a fundamental component of the hydrogeomorphic processes that create and
365 maintain riparian habitats (Steiger et al. 2005; Corenblit et al. 2009). Since we used a unified framework to
366 quantitatively compare the strategy-environment relationships of plants (Pierce et al. 2017), it will be
367 interesting to see whether the functional structure of riparian communities responds similarly to
368 environmental gradients in other systems. From a conservation or restoration perspective, riparian
369 communities in highly regulated rivers should benefit from (i) an increase in the intensity of disturbance
370 through the reactivation of bedload supply and transport (Bravard et al. 1999; Beechie et al. 2010), and (ii) an
371 increase in the intensity of stress through an increase in flow variability (e.g., increase flood events and favor
372 instable base-flow) (Greet et al. 2011; Tonkin et al. 2018). These actions would especially benefit the
373 development of ruderal pioneer communities in the tidal zone, which are the most threatened by the
374 overgrowth of competitive and stress-tolerant perennial species.

375

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380

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536

537 Table 1. Top-ranking models predicting the community-weighted mean values (CWM) and the functional
 538 dispersion values (FDis) of CSR plant strategies along the Rhône River (France), as assessed with Akaike's
 539 information criterion corrected for small sample size (AICc). Number of parameters (k), AICc, AICc weight (W)
 540 and adjusted marginal coefficient of determination (R^2) are provided.

Measure	Variable	Top-ranked model (fixed effects)	k	AICc	W	R^2_{marginal}
CWM	Competitive	Sediments	5	1044.7	0.267	0.041
	Stress-tolerant	Elevation + Temperature*Sediments	8	1243.6	0.238	0.097
	Ruderal	Temperature + Elevation*Sediments	8	1249.1	0.490	0.132
FDis	Competitive	Sediments	5	-184.2	0.296	0.104
	Stress-tolerant	Elevation + Temperature*Sediments	8	-66.6	0.415	0.148
	Ruderal	Elevation*Sediments	7	-8.7	0.413	0.138

541

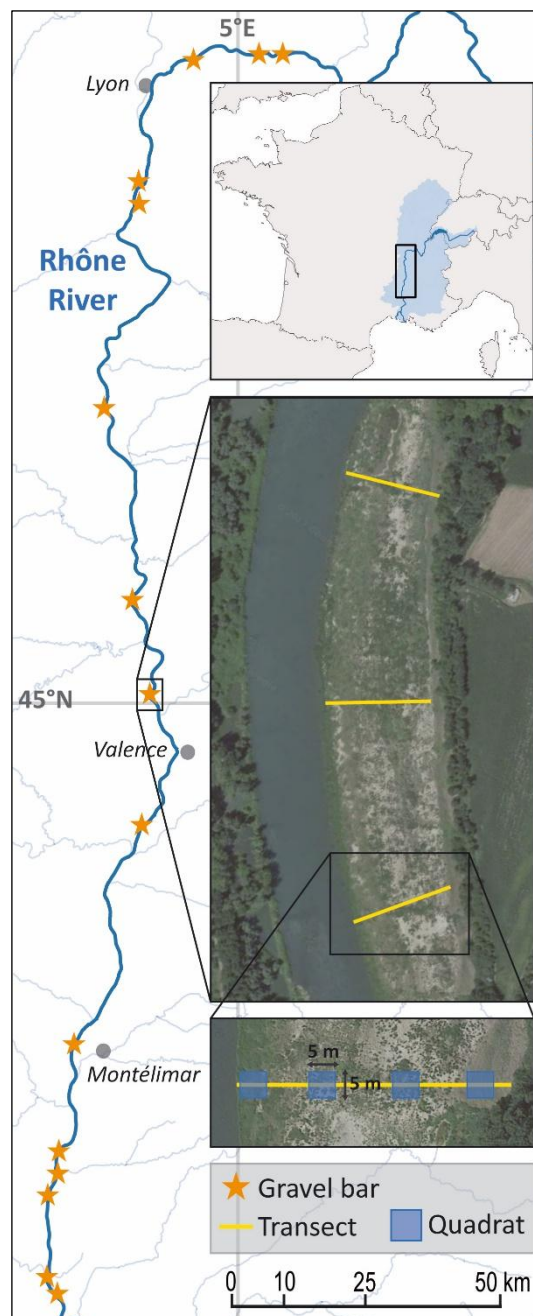
542 Table 2. Relative importance (Imp.), average coefficients (Estimate (\pm SE)) and confidence intervals (95% CI) for fixed effects used to predict the variation in the community-
 543 weighted mean values (CWM) and the functional dispersion values (FDis) of CSR plant strategies along the Rhône River (France). The 95% confidence intervals of
 544 coefficients in bold excluded 0 (NA = Not Available, i.e., AICc parameters and associated unconditional standard errors were not part of the top-ranked model).

Measure	Variable	Elevation			Sediments			Temperature		
		Imp.	Estimate (\pm SE)	(95% CI)	Imp.	Estimate (\pm SE)	(95% CI)	Imp.	Estimate (\pm SE)	(95% CI)
CWM	Competitive	0.42	-0.387 (\pm 0.371)	(-1.114; 0.340)	0.67	-0.272 (\pm 0.154)	(-0.575; 0.031)	0.30	-0.055 (\pm 0.874)	(-1.768; 1.658)
	Stress-tolerant	0.70	-1.187 (\pm 0.670)	(-2.500; 0.126)	0.79	0.430 (\pm 0.313)	(-0.183; 1.043)	0.81	-2.325 (\pm 1.800)	(-5.852; 1.202)
	Ruderal	0.95	1.562 (\pm0.660)	(0.268; 2.855)	0.78	-0.202 (\pm 0.284)	(-0.758; 0.355)	0.87	3.119 (\pm1.425)	(0.325; 5.912)
FDis	Competitive	0.33	-0.005 (\pm 0.012)	(-0.028; 0.019)	1.00	-0.017 (\pm0.006)	(-0.028; -0.005)	0.50	0.029 (\pm 0.028)	(-0.027; 0.084)
	Stress-tolerant	0.92	0.040 (\pm0.017)	(0.007; 0.072)	1.00	-0.034 (\pm0.009)	(-0.051; -0.016)	0.76	0.080 (\pm 0.042)	(-0.002; 0.163)
	Ruderal	1.00	0.052 (\pm0.020)	(0.013; 0.091)	1.00	-0.049 (\pm0.010)	(-0.069; -0.029)	0.54	0.054 (\pm 0.039)	(-0.022; 0.129)

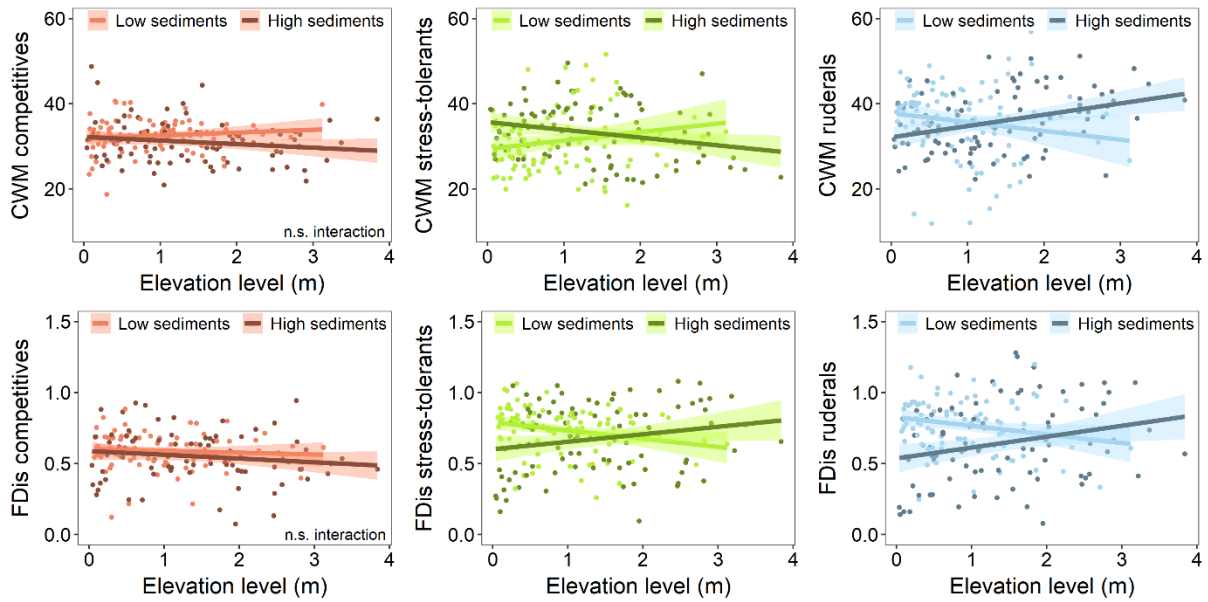
Measure	Variable	Elevation*Sediments			Elevation*Temperature			Sediments*Temperature		
		Imp.	Estimate (\pm SE)	(95% CI)	Imp.	Estimate (\pm SE)	(95% CI)	Imp.	Estimate (\pm SE)	(95% CI)
CWM	Competitive	0.06	-0.096 (\pm 0.133)	(-0.356; 0.164)	NA	NA	NA	0.07	-0.136 (\pm 0.154)	(-0.438; 0.165)
	Stress-tolerant	0.30	-0.513 (\pm0.227)	(-0.959; -0.068)	NA	NA	NA	0.39	0.622 (\pm0.269)	(0.096; 1.148)
	Ruderal	0.61	0.604 (\pm0.232)	(0.150; 1.058)	0.07	0.299 (\pm 0.601)	(-0.878; 1.477)	0.09	-0.468 (\pm 0.268)	(-0.993; 0.058)
FDis	Competitive	0.10	-0.006 (\pm 0.006)	(-0.016; 0.005)	NA	NA	NA	0.29	0.011 (\pm 0.006)	(-0.001; 0.023)
	Stress-tolerant	0.38	0.017 (\pm0.008)	(0.002; 0.032)	NA	NA	NA	0.52	0.022 (\pm0.009)	(0.005; 0.038)
	Ruderal	0.80	0.025 (\pm0.009)	(0.007; 0.042)	0.18	0.046 (\pm0.018)	(0.010; 0.081)	NA	NA	NA

545

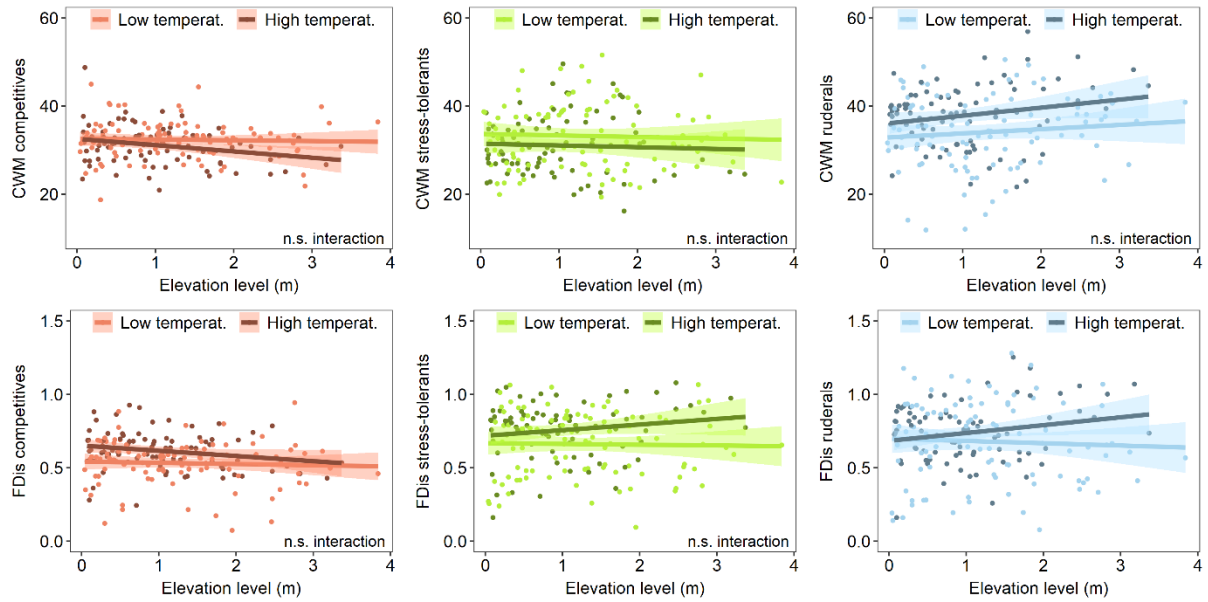
546 Figure 1. Location of the study area within the Rhône River watershed, distribution of sampled gravel bars
547 along the Rhône River and form of the sampling design used to survey riparian plant communities.



548 Figure 2. Interaction effect between elevation and sediments in relation to the community-weighted mean
549 values (CWM) and the functional dispersion values (FDis) of CSR plant strategies along the Rhône River
550 (France). To provide representation, the proportion of fine sediments has been divided into two equally sized
551 groups (see Table 2 for statistical significance, n.s. interaction = non-significant interaction).



552 Figure 3. Interaction effect between elevation and temperature in relation to the community-weighted mean
553 values (CWM) and the functional dispersion values (FDis) of CSR plant strategies along the Rhône River
554 (France). To provide representation, the mean annual temperature has been divided into two equally sized
555 groups (see Table 2 for statistical significance, n.s. interaction = non-significant interaction).



556 Figure 4. Interaction effect between sediments and temperature in relation to the community-weighted mean
557 values (CWM) and the functional dispersion values (FDis) of CSR plant strategies along the Rhône River
558 (France). To provide representation, the mean annual temperature has been divided into two equally sized
559 groups (see Table 2 for statistical significance, n.s. interaction = non-significant interaction).

