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Philippe Janssen, Hervé Piégay, André Evette

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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

6 Philippe Janssen<sup>1,2\*</sup>, Hervé Piégay<sup>2</sup>, André Evette<sup>1</sup>

7

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

9 <sup>2</sup> Univ. Lyon, UMR 5600 EVS, CNRS, ENS de Lyon, F-69342, Lyon, France

10

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

12

13 Email addresses of other authors:

14 H. Piégay ([herve.piegay@ens-lyon.fr](mailto:herve.piegay@ens-lyon.fr)), A. Evette ([andre.evette@inrae.fr](mailto:andre.evette@inrae.fr))

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 km<sup>2</sup>, mean  
114 annual discharge = 1,700 m<sup>3</sup>/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 19<sup>th</sup> 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 20<sup>th</sup> 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 m<sup>2</sup>) 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- $\mu$ 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  $\geq 0.95$  (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 =  $25.3 \pm 10.7$ ) were recorded in the 180 quadrats along the Rhône River:  
207 32 species ( $3.5 \pm 1.9$ ) were competitors (i.e., species C-dimensions  $> 50\%$ ), 39 species ( $4.1 \pm 2.4$ ) were stress-  
208 tolerators (i.e., species S-dimensions  $> 50\%$ ), 84 species ( $6.8 \pm 4.2$ ) were ruderals (i.e., species R-dimensions  $>$   
209  $50\%$ ), 62 species were not related to a dominant strategies ( $10.5 \pm 4.5$ ), 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

## 381 **REFERENCES**

- 382 Aguiar, F.C., Segurado, P., Martins, M.J., Bejarano, M.D., Nilsson, C., Portela, M.M., & Merritt, D.M. 2018. The  
383 abundance and distribution of guilds of riparian woody plants change in response to land use and flow  
384 regulation (M.-J. Fortin, Ed.). *Journal of Applied Ecology* 55: 2227–2240.
- 385 Asaeda, T., & Rashid, M.H. 2012. The impacts of sediment released from dams on downstream sediment bar  
386 vegetation. *Journal of Hydrology* 430–431: 25–38.
- 387 Asaeda, T., & Sanjaya, K. 2017. The effect of the shortage of gravel sediment in midstream river channels on  
388 riparian vegetation cover. *River Research and Applications* 33: 1107–1118.

389 Barton, K. 2015. *MuMIn: Multi-Model Inference. R package version 1.13.4.*

390 Bates, D., Mächler, M., Bolker, B., & Walker, S. 2015. Fitting Linear Mixed-Effects Models Using lme4. *Journal of*  
391 *Statistical Software* 67:.

392 Beechie, T.J., Sear, D.A., Olden, J.D., Pess, G.R., Buffington, J.M., Moir, H., Roni, P., & Pollock, M.M. 2010.  
393 Process-based Principles for Restoring River Ecosystems. *BioScience* 60: 209–222.

394 Bejarano, M.D., Nilsson, C., & Aguiar, F.C. 2018. Riparian plant guilds become simpler and most likely fewer  
395 following flow regulation (D. Moreno Mateos, Ed.). *Journal of Applied Ecology* 55: 365–376.

396 de Bello, F., Lavorel, S., Laverigne, S., Albert, C.H., Boulangeat, I., Mazel, F., & Thuiller, W. 2013. Hierarchical  
397 effects of environmental filters on the functional structure of plant communities: a case study in the  
398 French Alps. *Ecography* 36: 393–402.

399 Blom, C.W.P.M. 1999. Adaptations to flooding stress: from plant community to molecule. *Plant Biology* 1: 261–  
400 273.

401 Bravard, J.-P., & Gaydou, P. 2015. Historical development and integrated management of the Rhône River  
402 floodplain, from the Alps to the Camargue delta, France. In Hudson, P.F. & Middelkoop, H. (eds.),  
403 *Geomorphic approaches to integrated floodplain management of lowland fluvial systems in North*  
404 *America and Europe*, pp. 289–320. Springer New York, New York, NY.

405 Bravard, J.-P., Landon, N., Peiry, J.-L., & Piégay, H. 1999. Principles of engineering geomorphology for managing  
406 channel erosion and bedload transport, examples from French rivers. *Geomorphology* 31: 291–311.

407 Burnham, K.P., & Anderson, D.R. 2002. *Model selection and multi-model inference: a practical information-*  
408 *theoretic approach, 2nd ed.* Springer-Verlag, New York.

409 Butterfield, B.J., Palmquist, E., & Ralston, B. 2018. Hydrological regime and climate interactively shape riparian  
410 vegetation composition along the Colorado River, Grand Canyon. *Applied Vegetation Science* 21: 572–  
411 583.

412 Caccianiga, M., Luzzaro, A., Pierce, S., Ceriani, R.M., & Cerabolini, B. 2006. The functional basis of a primary  
413 succession resolved by CSR classification. *Oikos* 112: 10–20.

414 Capon, S.J., Chambers, L.E., Mac Nally, R., Naiman, R.J., Davies, P., Marshall, N., Pittock, J., Reid, M., Capon, T.,  
415 Douglas, M., Catford, J., Baldwin, D.S., Stewardson, M., Roberts, J., Parsons, M., & Williams, S.E. 2013.  
416 Riparian ecosystems in the 21st century: hotspots for climate change adaptation? *Ecosystems* 16: 359–  
417 381.



418 Corenblit, D., Steiger, J., Gurnell, A.M., Tabacchi, E., & Roques, L. 2009. Control of sediment dynamics by  
419 vegetation as a key function driving biogeomorphic succession within fluvial corridors. *Earth Surface*  
420 *Processes and Landforms* 34: 1790–1810.

421 Craft, C. 2016. *Creating and restoring wetlands: from theory to practice*.

422 Friedman, J.M., & Lee, V.J. 2002. Extreme floods, channel change, and riparian forests along ephemeral  
423 streams. *Ecological Monographs* 72: 409–425.

424 Garssen, A.G., Baattrup-Pedersen, A., Riis, T., Raven, B.M., Hoffman, C.C., Verhoeven, J.T.A., & Soons, M.B.  
425 2017. Effects of increased flooding on riparian vegetation: Field experiments simulating climate  
426 change along five European lowland streams. *Global Change Biology* 23: 3052–3063.

427 Garssen, A.G., Baattrup-Pedersen, A., Voesenek, L.A.C.J., Verhoeven, J.T.A., & Soons, M.B. 2015. Riparian plant  
428 community responses to increased flooding: a meta-analysis. *Global Change Biology* 21: 2881–2890.

429 Garssen, A.G., Verhoeven, J.T.A., & Soons, M.B. 2014. Effects of climate-induced increases in summer drought  
430 on riparian plant species: a meta-analysis. *Freshwater Biology* 59: 1052–1063.

431 González, E., González-Sanchis, M., Cabezas, Á., Comín, F.A., & Muller, E. 2010. Recent changes in the riparian  
432 forest of a large regulated mediterranean River: implications for management. *Environmental*  
433 *Management* 45: 669–681.

434 Greet, J., Angus Webb, J., & Cousens, R.D. 2011. The importance of seasonal flow timing for riparian vegetation  
435 dynamics: a systematic review using causal criteria analysis. *Freshwater Biology* 56: 1231–1247.

436 Grime, J.P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological  
437 and evolutionary theory. *The American Naturalist* 111: 1169–1194.

438 Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., & Jarvis, A. 2005. Very high resolution interpolated climate  
439 surfaces for global land areas. *International Journal of Climatology* 25: 1965–1978.

440 Kuglerová, L., Jansson, R., Sponseller, R.A., Laudon, H., & Malm-Renöfält, B. 2015. Local and regional processes  
441 determine plant species richness in a river-network metacommunity. *Ecology* 96: 381–391.

442 Kui, L., & Stella, J.C. 2016. Fluvial sediment burial increases mortality of young riparian trees but induces  
443 compensatory growth response in survivors. *Forest Ecology and Management* 366: 32–40.

444 Kyle, G., & Leishman, M.R. 2009. Plant functional trait variation in relation to riparian geomorphology: The  
445 importance of disturbance. *Austral Ecology* 34: 793–804.

446 Laliberté, E., & Legendre, P. 2010. A distance-based framework for measuring functional diversity from multiple  
447 traits. *Ecology* 91: 299–305.

448 Laliberté, E., Legendre, P., & Shipley, B. 2014. *FD: measuring functional diversity from multiple traits, and other*  
449 *tools for functional ecology. R package version 1.0-12.*

450 Lavorel, S., Grigulis, K., McIntyre, S., Williams, N.S.G., Garden, D., Dorrough, J., Berman, S., Quétier, F.,  
451 Thébault, A., & Bonis, A. 2008. Assessing functional diversity in the field – methodology matters!  
452 *Functional Ecology* 22: 134–147.

453 Li, Y., & Shipley, B. 2017. An experimental test of CSR theory using a globally calibrated ordination method.  
454 *PLOS ONE* 12: e0175404.

455 Lytle, D.A., & Poff, N.L. 2004. Adaptation to natural flow regimes. *Trends in Ecology & Evolution* 19: 94–100.

456 McCoy-Sulentic, M.E., Kolb, T.E., Merritt, D.M., Palmquist, E., Ralston, B.E., Sarr, D.A., & Shafroth, P.B. 2017.  
457 Changes in community-level riparian plant traits over inundation gradients, Colorado River, Grand  
458 Canyon. *Wetlands* 37: 635–646.

459 Merritt, D.M., & Poff, N.L.R. 2010. Shifting dominance of riparian *Populus* and *Tamarix* along gradients of flow  
460 alteration in western North American rivers. *Ecological Applications* 20: 135–152.

461 Nadal-Sala, D., Sabaté, S., Sánchez-Costa, E., Poblador, S., Sabater, F., & Gracia, C. 2017. Growth and water use  
462 performance of four co-occurring riparian tree species in a Mediterranean riparian forest. *Forest*  
463 *Ecology and Management* 396: 132–142.

464 Naiman, R.J., & Decamps, H. 1997. The ecology of interfaces: riparian zones. *Annual review of Ecology and*  
465 *Systematics* 28: 621–658.

466 Nakagawa, S., & Schielzeth, H. 2013. A general and simple method for obtaining  $R^2$  from generalized linear  
467 mixed-effects models. *Methods in Ecology and Evolution* 4: 133–142.

468 Nilsson, C., & Berggren, K. 2000. Alterations of riparian ecosystems caused by river regulation. *BioScience* 50:  
469 783.

470 Olden, J.D., & Rooney, T.P. 2006. On defining and quantifying biotic homogenization. *Global Ecology and*  
471 *Biogeography* 15: 113–120.

472 Perry, L.G., Andersen, D.C., Reynolds, L.V., Nelson, S.M., & Shafroth, P.B. 2012. Vulnerability of riparian  
473 ecosystems to elevated CO<sub>2</sub> and climate change in arid and semiarid western North America. *Global*  
474 *Change Biology* 18: 821–842.

475 Pierce, S., Negreiros, D., Cerabolini, B.E.L., Kattge, J., Díaz, S., Kleyer, M., Shipley, B., Wright, S.J., Soudzilovskaia,  
476 N.A., Onipchenko, V.G., van Bodegom, P.M., Frenette-Dussault, C., Weiher, E., Pinho, B.X., Cornelissen,  
477 J.H.C., Grime, J.P., Thompson, K., Hunt, R., Wilson, P.J., Buffa, G., Nyakunga, O.C., Reich, P.B.,  
478 Caccianiga, M., Mangili, F., Ceriani, R.M., Luzzaro, A., Brusa, G., Siefert, A., Barbosa, N.P.U., Chapin,  
479 F.S., Cornwell, W.K., Fang, J., Fernandes, G.W., Garnier, E., Le Stradic, S., Peñuelas, J., Melo, F.P.L.,  
480 Slaviero, A., Tabarelli, M., & Tampucci, D. 2017. A global method for calculating plant CSR ecological  
481 strategies applied across biomes world-wide. *Functional Ecology* 31: 444–457.

482 Poff, N.L., Allan, J.D., Bain, M.B., Karr, J.R., Prestegard, K.L., Richter, B.D., Sparks, R.E., & Stromberg, J.C. 1997.  
483 The natural flow regime. *BioScience* 47: 769–784.

484 Poff, N.L., Olden, J.D., Merritt, D.M., & Pepin, D.M. 2007. Homogenization of regional river dynamics by dams  
485 and global biodiversity implications. *Proceedings of the National Academy of Sciences* 104: 5732–5737.

486 Polzin, M.L., & Rood, S.B. 2006. Effective disturbance: Seedling safe sites and patch recruitment of riparian  
487 cottonwoods after a major flood of a mountain river. *Wetlands* 26: 965–980.

488 R Core Team. 2019. *R: A language and environment for statistical computing*. R Foundation for Statistical  
489 Computing, Vienna, Austria.

490 Reynolds, L.V., & Shafroth, P.B. 2017. Riparian plant composition along hydrologic gradients in a dryland river  
491 basin and implications for a warming climate. *Ecohydrology* 10: e1864.

492 Ricotta, C., & Moretti, M. 2011. CWM and Rao’s quadratic diversity: a unified framework for functional ecology.  
493 *Oecologia* 167: 181–188.

494 Rivaes, R., Rodríguez-González, P.M., Albuquerque, A., Pinheiro, A.N., Egger, G., & Ferreira, M.T. 2013. Riparian  
495 vegetation responses to altered flow regimes driven by climate change in Mediterranean rivers.  
496 *Ecohydrology* 6: 413–424.

497 Schielzeth, H. 2010. Simple means to improve the interpretability of regression coefficients: Interpretation of  
498 regression coefficients. *Methods in Ecology and Evolution* 1: 103–113.

499 Singer, M.B., Stella, J.C., Dufour, S., Piégay, H., Wilson, R.J.S., & Johnstone, L. 2013. Contrasting water-uptake  
500 and growth responses to drought in co-occurring riparian tree species. *Ecohydrology* 6: 402–412.

501 Solari, L., Van Oorschot, M., Belletti, B., Hendriks, D., Rinaldi, M., & Vargas-Luna, A. 2016. Advances on  
502 modelling riparian vegetation-hydromorphology interactions. *River Research and Applications* 32:  
503 164–178.

504 Steiger, J., & Gurnell, A.M. 2003. Spatial hydrogeomorphological influences on sediment and nutrient  
505 deposition in riparian zones: observations from the Garonne River, France. *Geomorphology* 49: 1–23.

506 Steiger, J., Tabacchi, E., Dufour, S., Corenblit, D., & Peiry, J.-L. 2005. Hydrogeomorphic processes affecting  
507 riparian habitat within alluvial channel-floodplain river systems: a review for the temperate zone. *River  
508 Research and Applications* 21: 719–737.

509 Stella, J.C., Riddle, J., Piégay, H., Gagnage, M., & Trémélo, M.-L. 2013. Climate and local geomorphic  
510 interactions drive patterns of riparian forest decline along a Mediterranean Basin river.  
511 *Geomorphology* 202: 101–114.

512 Stella, J.C., Rodríguez-González, P.M., Dufour, S., & Bendix, J. 2013. Riparian vegetation research in  
513 Mediterranean-climate regions: common patterns, ecological processes, and considerations for  
514 management. *Hydrobiologia* 719: 291–315.

515 Ström, L., Jansson, R., & Nilsson, C. 2012. Projected changes in plant species richness and extent of riparian  
516 vegetation belts as a result of climate-driven hydrological change along the Vindel River in Sweden.  
517 *Freshwater Biology* 57: 49–60.

518 Stromberg, J.C., Lite, S.J., & Dixon, M.D. 2009. Effects of stream flow patterns on riparian vegetation of a  
519 semiarid river: Implications for a changing climate. *River Research and Applications*. doi:  
520 10.1002/rra.1272

521 Stromberg, J.C., Setaro, D.L., Gallo, E.L., Lohse, K.A., & Meixner, T. 2017. Riparian vegetation of ephemeral  
522 streams. *Journal of Arid Environments* 138: 27–37.

523 Tonkin, J.D., Merritt, David.M., Olden, J.D., Reynolds, L.V., & Lytle, D.A. 2018. Flow regime alteration degrades  
524 ecological networks in riparian ecosystems. *Nature Ecology & Evolution* 2: 86–93.

525 Van Bodegom, P.M., Douma, J.C., Witte, J.P.M., Ordoñez, J.C., Bartholomeus, R.P., & Aerts, R. 2012. Going  
526 beyond limitations of plant functional types when predicting global ecosystem-atmosphere fluxes:  
527 exploring the merits of traits-based approaches. *Global Ecology and Biogeography* 21: 625–636.

528 Vázquez-Tarrío, D., Tal, M., Camenen, B., & Piégay, H. 2019. Effects of continuous embankments and successive  
529 run-of-the-river dams on bedload transport capacities along the Rhône River, France. *Science of The  
530 Total Environment* 658: 1375–1389.

531 Wilkes, M.A., Gittins, J.R., Mathers, K.L., Mason, R., Casas-Mulet, R., Vanzo, D., Mckenzie, M., Murray-Bligh, J.,  
532 England, J., Gurnell, A., & Jones, J.I. 2019. Physical and biological controls on fine sediment transport  
533 and storage in rivers. *Wiley Interdisciplinary Reviews: Water* 6: e1331.

534 Zimmermann, N.E., & Kienast, F. 1999. Predictive mapping of alpine grasslands in Switzerland: species versus  
535 community approach. *Journal of Vegetation Science* 10: 469–482.

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	$R^2_{\text{marginal}}$
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).

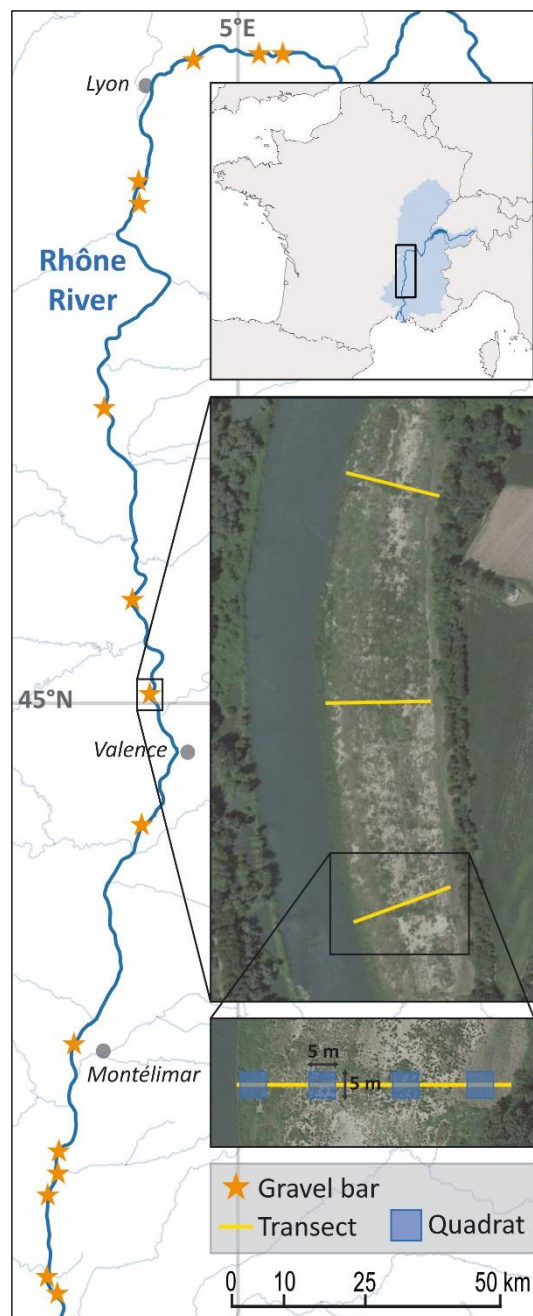
Measure	Variable	Elevation			Sediments			Temperature		
		Imp.	Estimate ( $\pm$ SE)	(95% CI)	Imp.	Estimate ( $\pm$ SE)	(95% CI)	Imp.	Estimate ( $\pm$ SE)	(95% CI)
CWM	Competitive	0.42	-0.387 ( $\pm$ 0.371)	(-1.114; 0.340)	0.67	-0.272 ( $\pm$ 0.154)	(-0.575; 0.031)	0.30	-0.055 ( $\pm$ 0.874)	(-1.768; 1.658)
	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	<b>0.95</b>	<b>1.562 (<math>\pm</math>0.660)</b>	<b>(0.268; 2.855)</b>	0.78	-0.202 ( $\pm$ 0.284)	(-0.758; 0.355)	<b>0.87</b>	<b>3.119 (<math>\pm</math>1.425)</b>	<b>(0.325; 5.912)</b>
FDis	Competitive	0.33	-0.005 ( $\pm$ 0.012)	(-0.028; 0.019)	<b>1.00</b>	<b>-0.017 (<math>\pm</math>0.006)</b>	<b>(-0.028; -0.005)</b>	0.50	0.029 ( $\pm$ 0.028)	(-0.027; 0.084)
	Stress-tolerant	<b>0.92</b>	<b>0.040 (<math>\pm</math>0.017)</b>	<b>(0.007; 0.072)</b>	<b>1.00</b>	<b>-0.034 (<math>\pm</math>0.009)</b>	<b>(-0.051; -0.016)</b>	0.76	0.080 ( $\pm$ 0.042)	(-0.002; 0.163)
	Ruderal	<b>1.00</b>	<b>0.052 (<math>\pm</math>0.020)</b>	<b>(0.013; 0.091)</b>	<b>1.00</b>	<b>-0.049 (<math>\pm</math>0.010)</b>	<b>(-0.069; -0.029)</b>	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	<b>0.30</b>	<b>-0.513 (<math>\pm</math>0.227)</b>	<b>(-0.959; -0.068)</b>	NA	NA	NA	<b>0.39</b>	<b>0.622 (<math>\pm</math>0.269)</b>	<b>(0.096; 1.148)</b>
	Ruderal	<b>0.61</b>	<b>0.604 (<math>\pm</math>0.232)</b>	<b>(0.150; 1.058)</b>	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	<b>0.38</b>	<b>0.017 (<math>\pm</math>0.008)</b>	<b>(0.002; 0.032)</b>	NA	NA	NA	<b>0.52</b>	<b>0.022 (<math>\pm</math>0.009)</b>	<b>(0.005; 0.038)</b>
	Ruderal	<b>0.80</b>	<b>0.025 (<math>\pm</math>0.009)</b>	<b>(0.007; 0.042)</b>	<b>0.18</b>	<b>0.046 (<math>\pm</math>0.018)</b>	<b>(0.010; 0.081)</b>	NA	NA	NA

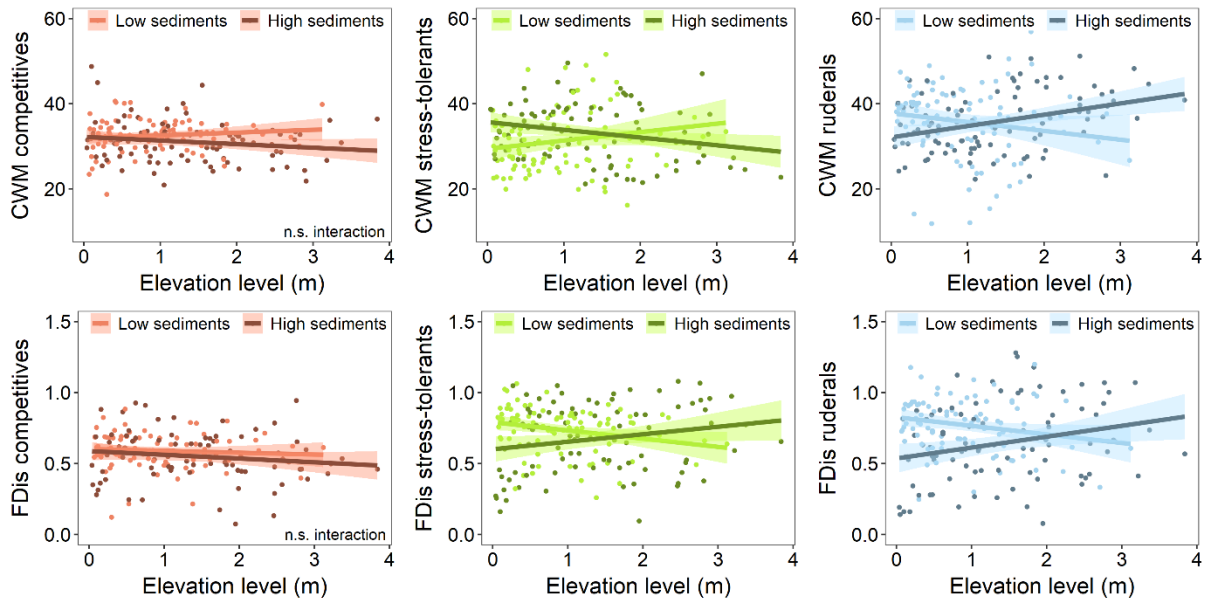
545

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.

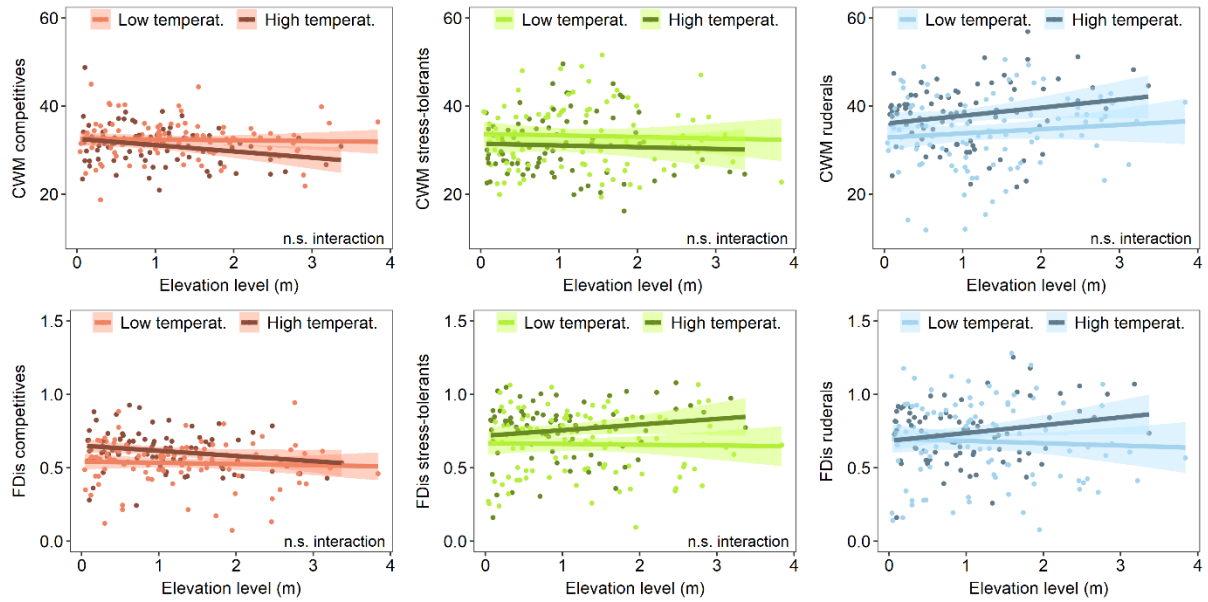




548 Figure 2. Interaction effect between elevation and sediments in relation to the community-weighted mean  
549 values (CWM) and the functional dispersion values (FDis) of CSR plant strategies along the Rhône River  
550 (France). To provide representation, the proportion of fine sediments has been 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).

