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1 **Long-term river management legacies strongly alter riparian forest attributes and constrain**
2 **restoration strategies along a large, multi-use river**

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22 **Abstract**

23 Many terrestrial ecosystems have undergone profound transformation under the pressure of
24 multiple human stressors. This may have oriented altered ecosystems toward transient or new
25 states. Understanding how these cumulative impacts influence ecosystem functions, services and
26 ecological trajectories is therefore essential to defining effective restoration strategies. This is
27 particularly the case in riverine ecosystems, where the profound alteration of natural disturbance
28 regimes can make the effectiveness of restoration operations questionable. Using the case study of
29 legacy dike fields, i.e., area delimited by longitudinal and lateral dikes, along the regulated Rhône
30 River, we studied the impacts of long-term channelization and flow regulation on environmental
31 conditions and riparian forests attributes along a 200km climatic gradient. We characterized the
32 imprint of human stressors on these forests by comparing the dike field stands to more natural
33 stands in both young and mature vegetation stages. Across four reaches of the river between Lyon
34 and the Mediterranean Sea, we found that channelization consistently promoted high rate of
35 overbank sedimentation and rapid disconnection of dike field surfaces from the channel. The rapid
36 terrestrialsation of dike field surfaces, i.e., the process by which former aquatic areas transition to a
37 terrestrial ecosystem as a result of dewatering or sedimentation, fostered a pulse of riparian forest
38 regeneration in these resource-rich environments that differs from more natural sites in structure
39 and composition. Within the dike fields, older pre-dam stands are dominated by post-pioneer and
40 exotic species, and post-dam stands support large, aging pioneer trees with a largely exotic
41 understory regeneration layer. These patterns were associated with differences in the relative
42 surface elevation among dike fields, whereas species shifts generally followed the river's longitudinal
43 climate gradient. To enhance the functionality of these human-made ecosystems, restoration
44 strategies should target the reconnection of dike fields to the river by dismantling part of the dikes to
45 promote lateral erosion, forest initiation and community succession, as well as increasing minimum
46 flows in channels to improve connection with groundwater. However, since a river-wide return to a
47 pre-disturbance state is very unlikely, a pragmatic approach should be favoured, focusing on local

48 actions that can improve abiotic and biotic function, and ultimately enhancing ecosystem services
49 such biodiversity, habitat, and recreation opportunities.
50 **Keywords:** Channelization, Ecological restoration, Flow regulation, Human-altered ecosystem,
51 Riparian forests, Rhône River

52 **1. Introduction**

53 Over recent decades, efforts to restore degraded ecosystems have vastly expanded in scope
54 and cost, with international ambitions rapidly increasing (e.g., Aichi Biodiversity Targets for 2011-
55 2020 set by the Convention on Biological Diversity). However, within many ecosystems, ecological
56 communities and functions may already be modified to the extent that they approach transient or
57 new states, i.e., “novel ecosystems”, making a return to the historical state difficult or impossible
58 (Hobbs et al., 2009). In many regions, cumulative human-induced stressors alter disturbance regimes,
59 modify abiotic conditions and/or favour the establishment of exotic species, leading to catastrophic
60 and irreversible shifts in both terrestrial and aquatic ecosystems properties (Scheffer et al., 2001).
61 These alterations may impair the ecological resilience of natural ecosystems and compromise their
62 ability to generate ecosystem services (Folke et al., 2004). Rapid and profound changes in both biotic
63 and abiotic conditions can impede efforts to restore highly altered ecosystems (Suding, 2011). Thus a
64 better understanding is needed of the capacity of these systems to provide sustainable habitats for
65 biodiversity, as well as other essential ecosystem functions.

66 Riparian ecosystems are among the environments most impacted by human activities (Best,
67 2019; Nilsson et al., 2005) and also those most vulnerable to ongoing global changes (Perry et al.,
68 2012). On many large rivers, massive civil engineering projects in the form of dikes, diversions, dams
69 and reservoirs have been constructed to exploit surface water supplies, control the risk of flooding
70 and bank erosion, improve river navigation, and protect infrastructure, among other functions. As a
71 result, in many parts of the world, riparian ecosystems currently comprise a mixture of historic-relict,
72 hybrid and novel ecosystems (Cooper and Andersen, 2012; Johnson, 2002). Due to the magnitude of
73 biotic alterations as well as their drivers, these cumulative changes can potentially compromise the
74 success of restoration objectives (Richardson et al., 2007).

75 To improve habitat and water quality along riparian zones, large-scale river restoration
76 programs have become a major objective for many European countries (e.g., in implementing the
77 European Water Framework Directive of 2000). Through removing dikes, adding sediment, raising

78 minimum flow levels, and augmenting natural aspects of regulated flow regimes (i.e., “ecological
79 flows”), river managers aim to restore physical processes such as bank erosion, bedload transport,
80 and floodplain inundation (Biron et al., 2014; Rohde et al., 2005), and thus reorient altered systems
81 toward their historical reference trajectories or a more dynamic stage. However, given the profound
82 alteration of natural disturbance regimes and modifications to biotic and abiotic conditions induced
83 by human infrastructure, the real added-value of these restoration actions is questionable (Dufour
84 and Piégay, 2009). Indeed, due to widespread and irreversible land-use change on floodplains in
85 conjunction with the incompatibility of ambitious restoration approaches with current human
86 demand, the capacity of these degraded ecosystems to provide sustainable habitats and important
87 ecosystem services into the future needs to be further studied and justified (e.g., Henning and
88 Hentschel, 2013; Shields, 1995; Simons et al., 2001; Thorel et al., 2018).

89 Here, we aimed to understand the cumulative impact of human-induced stressors on the
90 structure and composition of riparian forests. While interactions between shifting river landscapes
91 and riparian forest attributes has been relatively well studied (Cooper et al., 2003; Johnson et al.,
92 1976; Stella et al., 2011), there is a dearth of understanding how highly modified river-floodplain
93 systems respond to multiple stressors operating at the timeframes of decades to centuries (Reid et
94 al., 2019). Most of the studies available in the literature have either investigated the individual effect
95 of channelization (Dufour et al., 2007; Nakamura et al., 2002; Oswalt and King, 2005) or the
96 individual effect of flow regulation (Bejarano et al., 2018; Kui et al., 2017; Merritt and Cooper, 2000)
97 on riparian communities. In this study, we focused on the cumulative impact of these two human-
98 made alterations on riparian communities, using a nested sampling design in which we studied
99 variations in forest attributes along a large, extensively channelized river, while contrasting the
100 stages of development before and after the construction and operation of local flow-regulation
101 dams. Moreover, by adopting a comparative approach among four reaches along a north-south river
102 corridor, extending from a Continental to Mediterranean climate, we assessed both the effect of the
103 longitudinal climatic gradient and local reach effects on the structure and composition of riparian

104 forests. Such information is essential to understand how local factors influence stand development
105 and therefore to adapt management strategies to the specificities of the river reach and prioritize
106 areas with high restoration potential.

107 Our study is focused on the floodplains of the lower Rhône River (France), where engineered
108 dike fields were constructed along both riverbanks in the middle 19th Century to constrain the river
109 and improve commercial navigation (Thorel et al., 2018). Since the middle 20th Century, a second
110 human stressor was imposed on the river in the form of a chain of hydroelectric dams and bypass
111 channels. These developments have fundamentally altered the river's flow configuration and
112 discharge regime in the bypassed reaches, i.e., the historical Rhône River channel running parallel to
113 a diversion canal, where the earlier dike fields have gradually transitioned to riparian forest. Within
114 these dammed and bypassed reaches, we used dike field surfaces as a case study to highlight the
115 relative influence of channelization and flow regulation on riparian forest attributes and characterize
116 more broadly the overall imprint left by these human-induced stressors on the Rhône River riparian
117 zone. This was done to evaluate the future capacity of these highly modified/novel ecosystems to
118 provide sustainable riparian habitat, and to determine the potential ecological benefits of
119 dismantling the engineered structures as part of a river-wide restoration program (Thorel et al.,
120 2018). Though the particular configuration, timing and scale of the river transformation is specific to
121 the Rhône River, the fact that these same influences have been imposed on many large, multi-use
122 rivers in Europe (e.g., Arnaud et al., 2015; Hein et al., 2016), North America (e.g., Alexander et al.,
123 2012; Johnson et al., 2015) and elsewhere (e.g., Luan et al., 2018; Wohl, 2019) highlights the
124 applicability of this study to other regions globally.

125 Based on this context of cumulative human stressor effects on riverine systems, we
126 addressed the following four research objectives: (i) How environmental conditions vary between
127 pre-dam and post-dam surfaces as well as among bypassed reaches; (ii) How the structure and
128 composition of dike field forests vary between pre-dam and post-dam surfaces as well as among
129 bypassed reaches; (iii) How the structure and composition of dike field forests vary with

130 environmental variables describing hydro-geomorphic and climatic gradients; (iv) How the structure
131 and composition of dike field forests differ from that of young and mature riparian forests in more
132 natural environments within the same biogeographic region.

133

134 **2. Material and Methods**

135 **2.1. Study area**

136 The study was carried out along the Rhône River (total length = 810 km, catchment area =
137 96,500 km², mean annual discharge = 1,700 m³ s⁻¹) in southeastern France (Figure 1). Comparable to
138 other large rivers, the Rhône Basin has been subject to multiple uses since early settlement, including
139 agriculture, forestry and gravel extraction. In the last two centuries, two extensive river engineering
140 phases profoundly changed its course and its hydro-sedimentary and ecological functioning. During
141 the 19th Century, an extensive system of longitudinal and lateral submersible stone dikes was
142 constructed to aid river navigation in the main channel downstream of Lyon. The long chains of
143 rectangular compartments, referred to as “dike fields”, concentrated the flow into a single-thread
144 channel by damming secondary channels during low flows and fixing the position of pools and riffles.
145 During the second half of the 20th Century following World War II, an ambitious program of
146 economic recovery was initiated within the Rhône River corridor and a total of twenty-four dams and
147 hydro-electric power plants were constructed. Of these, sixteen dams feature diversion canals,
148 excavated in parallel to the natural river course, creating secondary bypass channels in these reaches
149 (total length = 162 km, Lamouroux et al., 2015). The diversion dams distribute the largest part of the
150 discharge into the canals, while the bypassed reaches receive only a minimum baseflow discharge
151 (i.e., residual flow is 10 to 30% of the mean annual flow arriving at the upstream diversion dams)
152 (Vázquez-Tarrío et al., 2019).

153 In the post-dam period, the dike fields have served as efficient sediment traps, and the
154 accumulated overbank fine sediments have shifted the river margins from an aquatic to
155 predominately terrestrial state (hereafter referred to as terrestrialisation), especially in the bypassed

156 reaches (Räpple, 2018; Thorel et al., 2018). Prior to the dam construction period, terrestrialisation
157 occurred gradually over several decades due to sediment filling; however this rate abruptly increased
158 during the bypassing period due to reductions in baseflow and dewatering within the dike fields
159 (Appendix 1). Two distinct stages of surface and forest development are thus distinguished, pre- and
160 post-dam. The predominant land cover in the bypassed reaches is today mostly composed of riparian
161 forests. Their species pool includes both pioneer, dominated by *Salix alba*, *Populus nigra* and *P. alba*,
162 and post-pioneer species, dominated by *Fraxinus angustifolia*, as well as abundant exotic species,
163 dominated by *Acer negundo* and *Robinia pseudoacacia* (Janssen et al., 2020).

164 **2.2. Dike field forest inventory**

165 The study sites comprised four bypassed reaches between Lyon and the Mediterranean Sea.
166 Pierre-Bénite (PBN) and Péage de Roussillon (PDR) are located in the upstream part and experience a
167 continental/oceanic climate; Montélimar (MON) and Donzère-Mondragon (DZM) lie further
168 downstream within the Mediterranean climate zone (Figure 1). For each study reach, we used geo-
169 referenced aerial photograph series in a Geographic Information System (ESRI ArcMap 10.3) to
170 manually delineate surfaces within the dike fields, which are exposed and evident over an extended
171 period of the year (see Appendix 1). We selected one aerial image series per reach, which was closest
172 prior to the year of dam construction (i.e., PBN = 1966, PDR = 1977, MON = 1957, DZM = 1952) and
173 covered the entire reach to delineate “pre-dam surfaces”. A set of post-2000 orthophotographs was
174 used to delineate “post-dam surfaces” that had emerged following diversion. Finally, we superposed
175 the resulting surface polygons of the two years to create a ‘surface age’ map (see Appendix 2 for
176 details).

177 Overlaying the forest stand polygons and the surface age map, we selected 61 dike fields
178 among the four bypassed reaches. We then used a stratified random approach to distribute 42
179 sampling plots in pre-dam dike field surfaces (PBN = 11, PDR = 10, MON = 10, DZM = 11) and 40
180 sampling plots in post-dam dike field surfaces (PBN = 10, PDR = 10, MON = 10, DZM = 10), while
181 avoiding sampling the elevated stone dike structures themselves. For each forest plot, the forest

182 inventory and the measurement of environmental variables were done in spring 2014 within two
183 nested concentric plot sizes: a 10-m radius plot (area: 314 m²) for recording all live and dead standing
184 trees with a diameter at breast height (DBH) ≥ 7.5 cm, and a 20-m radius plot (area: 1,256 m²) for
185 recording all live and dead standing trees with DBH ≥ 30 cm. Furthermore, three sub-plots of 1.5-m
186 radius each (7 m²) were centered on the 10-m radius plot perimeter, positioned at due North and at
187 133 and 267 degrees radially, to inventory regeneration stems (i.e., DBH < 7.5 cm). For each tree, we
188 recorded species, DBH and health class, comprising live trees (< 50% dead crown and branches),
189 dying trees (>50% dead crown and branches), or dead trees.

190 To compare stand attributes between the study sites, data were standardized to a per
191 hectare basis. Basal area (m² ha⁻¹), mean diameter (cm) and stem density (stems ha⁻¹) were
192 calculated for total live standing trees, distinguishing between overstorey (i.e., DBH ≥ 7.5 cm) and
193 understorey (i.e., DBH < 7.5 cm) vegetation and among pioneer, post-pioneer and exotic tree species
194 (see Appendix 3 for details).

195 **2.3. Environmental variables**

196 To assess conditions relative to the provision and accessibility of resources to the trees, as
197 well as relative to the disturbance level, we measured fine sediment depth (median grain size $\phi \leq 2$
198 mm) at each plot centre. We assumed that the fine grain-dominated material was deposited on top
199 of coarse-grained material, which made up the former river channel or had accumulated in the initial
200 phase following dike construction, when the dike field's connectivity to the main channel was still
201 frequent. Using a soil corer ($\phi = 5$ cm), we penetrated the ground until a dull sound and an increased
202 resistance was perceived, which was assumed to reflect the gravel layer boundary, and measured
203 that distance from the surface. To characterize the climatic gradient along the north-south Rhône
204 River corridor, extending across a Continental to Mediterranean climate, we recorded the geographic
205 coordinates (longitude and latitude) at the centre of each plot using a high-accuracy GPS (Trimble
206 GEO7X). To describe the hydrological connectivity, we used two correlated variables (see Appendix 4
207 for correlation matrix), the relative surface elevation above the water level at a discharge of 100 m³ s⁻¹

208 ¹ and the inundation duration (in days per year). Values were extracted value at each plot centre
209 from the models of Džubáková et al. (2015), which used ground elevation based on airborne LiDAR
210 data and digital elevation models, combined with flow levels observed from field reconnaissance.
211 Only the upper Rhône reaches, notably PBN, were shown in the Džubáková et al.'s paper (2015) but
212 PDR, DZM and MON were also available.

213 **2.4. Young and mature forest inventories**

214 We used two complementary datasets to compare the structure and composition of dike
215 field forests with those of riparian forests less impacted by human activities and located in the same
216 biogeographic region. For comparison to a young vegetation stage, we used a 2001 inventory of
217 woody vegetation on the Drôme River (hereafter DRO), a tributary of the Rhône in southeastern
218 France (Dufour et al., 2007). The inventory was conducted across four young vegetation islands
219 within the active floodplain of the river with quadrats of 4 m² (2 m x 2 m) distributed along transects
220 that bisected the islands, and within which all tree species and stem diameters measuring 5 cm
221 above ground level were recorded. To make forest inventories more comparable between the Rhône
222 and Drôme rivers, we accumulated the 4 m² quadrat surfaces by considering the downstream,
223 upstream and intermediate zone of each island (n = 12, mean ±SD = 34.3 ±19.3 m², range: 12–44 m²).
224 For comparison to a mature vegetation stage characteristic of the older end of the floodplain
225 vegetation chronosequence, we used a 2013 riparian forest inventory within the Natural Reserve of
226 the “Ile de la Platière” (hereafter PLA). The reserve is located within the bypassed reach of Péage de
227 Roussillon and forest inventories were conducted within naturally-established floodplain stands (i.e.,
228 not within dike fields) using the same protocol adopted in the current study.

229 **2.5. Statistical analysis**

230 All analyses were conducted with R version 3.6.1 (R Core Team, 2020).

231 **2.5.1. Variation in environmental conditions between pre-dam and post-dam surfaces, and among** 232 **bypassed reaches**

233 We used one-way ANOVAs with type III sum of squares and Tukey's HSD post hoc tests to
234 assess whether surface elevation, inundation duration, fine sediment depth and surface age varied
235 between pre- and post-dam surfaces and bypassed reaches. Prior to analysis, the variable inundation
236 duration was log+1 transformed to approximate normal distribution. In addition, we used linear
237 regression to determine how environmental variables varied with surface age and whether these
238 trends were consistent among bypassed reaches. We fitted normal linear models (LMs) or lognormal
239 LMs for skewed variables (i.e., inundation duration) and tested for an interaction effect between
240 surface age and the bypassed reach factor (see Appendix 6 for model construction).

241 **2.5.2. Variation in structure and composition of dike field forests between pre-dam and post-dam** 242 **surfaces, and among bypassed reaches**

243 We used one-way ANOVAs with type III sum of squares and Tukey's HSD post hoc tests to
244 assess whether the structure of the dike field forests varied between pre- and post-dam surfaces and
245 bypassed reaches. The analyses distinguished between basal area, stem density and mean diameter
246 of pioneer, post-pioneer, and exotic trees within both the understorey and overstorey separately
247 (Appendix 3). Since almost all of these variables were more or less over-dispersed, they were either
248 log or log+1 transformed prior to analysis.

249 We used multivariate generalized linear models (GLMs) to identify variations in tree species
250 composition between pre-dam/post-dam surfaces and bypassed reaches. This approach has the
251 advantage of being based on a GLM framework, which is robust to the strong mean-variance
252 relationship in multivariate data (Warton et al., 2012). We used the 'manyglm' function of the
253 'mvabund' package (Wang et al., 2012) to fit negative binomial regressions to each tree species that
254 were present in more than 5% of the plots, using integer values of basal area as an abundance
255 measure, and summed the likelihood ratio statistics to estimate their multivariate response. The
256 significance of each independent variable in the multivariate GLM was assessed using an analysis of
257 variance with the PIT-trap method and 999 bootstrap resamples (Warton et al., 2017). Model
258 performance was evaluated according to the proportion of deviance explained ($D^2 = [\text{null deviance} -$

259 residual deviance]/null deviance). When factors had more than two levels, pairwise comparisons
260 between each level were performed, adjusting for multiple comparisons via a free stepdown
261 resampling procedure, to identify the factor levels that showed statistically significant differences in
262 forest composition. To determine which tree species contributed most to the overall model
263 deviance, we extracted univariate test statistics and p-values, adjusted to correct for multiple tests
264 for each species. Finally, to provide a graphical representation of the gradients in forest composition,
265 we used a canonical analysis of principal coordinates (Anderson and Willis, 2003), using a Bray-Curtis
266 distance.

267 **2.5.3. Variation in structure and composition of dike field forests along hydro-geomorphic and** 268 **climatic gradients**

269 We used lognormal linear regression models to assess the individual effects of latitude (a
270 proxy for the climate gradient), relative surface elevation, inundation duration, fine sediment depth
271 and surface age on the same stand structure variables as above. We ranked the five models, plus a
272 null model, using the Akaike's information criterion corrected for small sample sizes. Because some
273 values of relative surface elevation and inundation duration were missing, we modeled them using
274 the output of the previous linear models. Then, we extracted for each parameter the estimate and
275 associated standard errors, as well as the 95% confidence intervals.

276 We used multivariate GLMs to identify variations in tree species composition with relative
277 surface elevation, inundation duration, surface age, fine sediments depth and latitude. Then, as
278 detailed above, we extracted information on the significance of each independent variable, the
279 proportion of deviance explained and the univariate test statistics and p-values.

280 **2.5.4. Differences in dike field forest structure and composition from young and mature riparian** 281 **stands**

282 We used one-way ANOVAs with type III sum of squares and Tukey's HSD post hoc tests to
283 assess whether the structure of the dike field forests differed from those of young and mature

284 vegetation stages. Response variables were the same as for the inter-site comparisons, with dike
285 fields split between pre- and post-dam surfaces represented as a single level factor.

286 We used multivariate GLMs to identify variations in tree species composition between dike
287 fields, young and mature vegetation stages. Then, as detailed above, we extracted information on
288 the significance of each independent variable, the proportion of deviance explained and the
289 univariate test statistics and p-values.

290

291 **3. Results**

292 **3.1. Variation in environmental conditions between pre-dam and post-dam surfaces, and among** 293 **bypassed reaches**

294 One-way ANOVA revealed that elevation, fine sediment depth and surface age significantly
295 decreased between pre-dam and post-dam surfaces, whereas the inundation duration significantly
296 increased (Figure 2; Appendix 5). Among bypassed reaches, the inundation duration, surface
297 elevation and fine sediment depth also varied significantly (Appendix 5). Tukey HSD tests revealed
298 that the average surface elevation was significantly lower and the inundation duration significantly
299 greater within the PDR reach. Also, the fine sediment depth was significantly greater within the DZM
300 reach (Figure 2).

301 Linear regression revealed no significant interaction between surface age and bypassed
302 reaches for all environmental variables (Figure 3; Appendix 6). The relative surface elevation
303 increased with surface age, while the inundation duration decreased. Also, the inundation duration
304 was significantly lower and the fine sediment depth significantly greater within the DZM reach as
305 compared to the PBN reach.

306 **3.2. Variation in structure and composition of dike field forests between pre-dam and post-**
307 **dam surfaces, and among bypassed reaches**One-way ANOVA revealed that the stem density and the
308 basal area of post-pioneer trees, as well as the basal area and the mean diameter of exotic trees in
309 the overstorey significantly decreased between pre-dam and post-dam surfaces (Figure 4; Appendix

310 7). Conversely, the stem density of pioneer trees in the overstorey significantly increased between
311 pre-dam and post-dam surfaces. One-way ANOVA also revealed significant differences in stem
312 density of pioneer trees and basal area of exotic trees in the understorey as well as in stem density
313 and basal area of pioneer and exotic trees in the overstorey between bypassed reaches (Appendix 7).
314 Tukey HSD tests revealed that the stem density of pioneer trees and the basal area of exotic trees in
315 the understorey were significantly higher on the MON reach (Figure 4). For the overstorey, the stem
316 density of pioneer trees was significantly higher on the PDR reach and the basal area of pioneer trees
317 was significantly higher on the PDR and MON reaches. Also, the stem density and the basal area of
318 exotic trees were significantly higher on the DZM reach, whereas the mean diameter was
319 significantly higher on the PBN reach.

320 Multivariate GLM revealed that tree species composition varied significantly between post-
321 dam and pre-dam surfaces (Dev = 42, $p = 0.001$), bypassed reaches (Dev = 140, $p = 0.001$) and their
322 interaction term (Dev = 96, $p = 0.001$), while explaining a large part of the variation ($D^2 = 0.392$).
323 Pairwise comparisons revealed significant differences in tree composition between all pairs of
324 bypassed reaches. Univariate tests ($n = 16$, Appendix 11) showed that the abundance of *Ligustrum*
325 *vulgare* (Dev = 8, $p\text{-adj} = 0.050$) increased on pre-dam surfaces and that of *Acer negundo* (Dev = 16,
326 $p\text{-adj} = 0.020$) increased in the PBN, MON and DZM reaches (Figure 7). Finally, the abundance of *Salix*
327 *alba* (Dev = 21, $p\text{-adj} = 0.004$) increased on post-dam surfaces, in the central part of the Rhône
328 corridor, while the abundance of *Sambucus nigra* (Dev = 14, $p\text{-adj} = 0.044$) increased on pre-dam
329 surfaces, in the southern part.

330 **3.3. Variation in structure and composition of dike field forests along hydro-geomorphic and** 331 **climatic gradients**

332 Linear regressions revealed that the model including the relative surface elevation ranks first
333 for 9 of the 18 stand structure variables (Table 1; Appendix 8). An increase in the surface elevation
334 induced a significant increase in the density, basal area and, to lower extent, mean diameter of post-
335 pioneer and exotic trees but a significant decrease in the density and basal area of pioneer trees,

336 especially in the overstorey (Figure 5; Appendix 9). The surface age and fine sediment depth had a
337 similar effect on the structure of dike field forests, while the inundation duration had the opposite
338 effect. However, as evaluated by the adjusted coefficient of determination (Appendix 8), the effect
339 size of these variables was of lower importance than the one related to surface elevation. Finally, as
340 latitude decreased, the density and basal area of exotic trees increased significantly.

341 Multivariate GLM revealed that tree species composition varied significantly with latitude
342 (Dev = 54, $p = 0.001$), inundation duration (Dev = 83, $p = 0.001$) and relative surface elevation (Dev =
343 48, $p = 0.001$), but not with surface age (Dev = 11, $p = 0.852$) and fine sediment depth (Dev = 17, $p =$
344 0.524). Altogether, these variables explained a large part of the variation ($D^2 = 0.352$). Univariate
345 tests ($n = 15$, Appendix 12) showed that the abundance of *Ligustrum vulgare* (Dev = 12, $p\text{-adj} = 0.006$)
346 increased in the northern part of the study area while that of *Populus alba* (Dev = 13, $p\text{-adj} = 0.004$)
347 increased in the southern part (Figure 7). Moreover, the abundance of *Acer negundo* (Dev = 12, $p\text{-adj}$
348 = 0.016), *Cornus sanguinea* (Dev = 15, $p\text{-adj} = 0.004$), *Juglans regia* (Dev = 10, $p\text{-adj} = 0.032$),
349 *Ligustrum vulgare* (Dev = 14, $p\text{-adj} = 0.004$) and *Robinia pseudoacacia* (Dev = 14, $p\text{-adj} = 0.004$)
350 increased in non-flooded surfaces. Finally, the abundance of *Salix alba* (Dev = 15, $p = 0.011$)
351 increased at low elevation.

352 **3.4. Differences in dike field forest structure and composition from young and mature riparian** 353 **stands**

354 One-way ANOVA revealed that most stand structure variables varied significantly between
355 dike-fields, young and mature vegetation stages (Figure 6; Appendix 10). Tukey HSD tests revealed
356 that the young stage had higher basal area and higher density of pioneer trees. Conversely, the
357 mature stage had higher density and basal area of post-pioneer trees. Also, for pioneer trees in the
358 overstorey, the mean diameter was significantly higher in dike field forests and mature stage, while
359 the basal area was significantly higher only in dike fields forests. Dike field forests also had
360 significantly higher overstorey density and basal area of exotic trees.

361 Multivariate GLM revealed that tree species composition varied significantly between dike
362 fields, young and mature stages (Dev = 579, $p = 0.001$, $D^2 = 0.429$). Pairwise comparisons showed

363 significant difference in species composition between all pairs of forest types. Univariate tests (n =
364 17, Appendix 13) showed that nearly all species contributed to the multivariate effect. As such, the
365 abundance of *Salix eleagnos* (Dev = 80, *p-adj* = 0.001), *Salix purpurea* (Dev = 58, *p-adj* = 0.001) and
366 *Populus nigra* (Dev = 7, *p-adj* = 0.038) increased in the young stage; the abundance of *Crataegus*
367 *monogyna* (Dev = 96, *p-adj* = 0.001), *Fraxinus angustifolia* (Dev = 51, *p-adj* = 0.001) and *Ligustrum*
368 *vulgare* (Dev = 43, *p-adj* = 0.001) in the mature stage; and the abundance of *Salix alba* (Dev = 57, *p-*
369 *adj* = 0.001), *Acer negundo* (Dev = 47, *p-adj* = 0.001) and *Populus alba* (Dev = 8, *p-adj* = 0.036) in dike
370 field forests (Figure 7).

371

372 **4. Discussion**

373 Most of the terrestrial biosphere has been transformed by anthropogenic drivers into hybrid
374 human/natural ecosystems (Ellis et al., 2010). Identifying the drivers that lead to the degradation or
375 divergence of ecosystems to novel states is essential for proper ecosystem assessment and
376 management (Morse et al., 2014). Using the case study of the highly regulated Rhône River, we
377 showed that the cumulative impact of channelization and flow regulation induced major changes in
378 environmental conditions and in riparian forest attributes. Specifically, there are strong differences in
379 environmental conditions between pre-dam and post-dam surfaces, but less variation amongst river
380 reaches, demonstrating the greater effect on riparian forest trajectories of different river
381 management regimes compared to the river's longitudinal climatic and hydro-geomorphic gradient.
382 Several environmental variables, especially the relative elevation of dike field surfaces, strongly
383 influenced the structure of riparian forests, while their composition was principally influenced by the
384 stands' position along the Continental to Mediterranean climate gradient within the Rhône River
385 corridor. Compared to more natural, young and mature riparian forests, the dike-field forests were
386 characterized by the dominance of very large, aging pioneer trees, but also more exotic trees.
387 Overall, our results indicate that the artificial structures facilitated a homogenization of

388 environmental conditions along the Rhône, favouring the development of stands that differ in
389 structure and composition from riparian forests within the same biogeographic setting.

390 **4.1. Channelization and flow regulation influences on dike field environmental conditions**

391 Strong differences in environmental conditions between pre-dam and post-dam surfaces
392 were evident within the bypassed reaches of the Rhône River. Older pre-dam surfaces have a higher
393 relative elevation, greater accumulation of fine sediment and are less prone to flooding during the
394 year. Because these surfaces are older and have experienced a long flood history, they have had time
395 to accumulate more sediment than younger surfaces. Also, the capacity of dike fields to trap
396 suspended sediment has been shown to be greatest immediately after their completion, after which
397 sedimentation rates decreased over time (Tena et al., 2020). As in natural floodplains, these results
398 confirm the natural attenuation of sediment deposition over time, even within the artificial
399 structures. However, our results also indicate that fine sediments depth was not predicted by surface
400 age, meaning that terrestrialisation does not rely solely on deposition. Indeed, river incision has been
401 emphasized as an important factor in driving floodplain terrestrialisation along the Rhône River
402 (Provansal et al., 2014; Tena et al., 2020), as well as along other channelized rivers (e.g., Habersack et
403 al., 2016; Surian and Rinaldi, 2003; Wyżga, 2001). Therefore, the sudden transition from coarse-
404 grained to fine-grained sediments and connectivity between the floodplain and the channel reflects
405 the combined effect of overbank fine sedimentation and channel incision, mainly operating during
406 the river's channelization phase (Petit et al., 1996; Provansal et al., 2014; Vauclin et al., 2019).
407 Overall, this shows that dike fields created relatively homogeneous environmental conditions to the
408 detriment of floodplain heterogeneity and connectivity (Franklin et al., 2009), which are essential
409 components in maintaining the ecological diversity of riparian zones (Naiman et al., 2005; Poff et al.,
410 1997). In accordance with James (2017), we inferred that dike field structures and subsequent flow
411 regulation are anthropogenic inhibitors that have altered the natural channel and floodplain
412 geomorphic trajectory, resulting in highly stable environmental conditions along the channelized
413 Rhône River margins.

414 Although changes in environmental conditions varied consistently between pre-dam and
415 post-dam surfaces, differences in abiotic conditions did occur across the four bypassed reaches
416 studied. Dike fields were at significantly lower elevation on the Péage de Roussillon reach (PDR),
417 which induces more frequent flood events in this bypassed section, while fine sediments depth was
418 greater on the Donzère Mondragon reach (DZM). For PDR specifically, this local response is due to
419 the fact that this bypassed reach is less incised, i.e., shear stress is compensated by upstream
420 sediment supply, and thus more connected to the channel (Tena et al., 2020). The downstream
421 increase in sediment thickness, with the greatest values at the DZM reach (Figure 2), reflects the
422 progressively larger sediment flux to the mainstem Rhône from its tributaries, primarily the Isère
423 River (Dépret et al., 2017; Poulhier et al., 2019). Combined with channel incision, a high rate of
424 overbank sedimentation has induced a major disconnection of the dike field surfaces, particularly in
425 the bypassed DZM reach (Tena et al., 2020). This spatial variation in environmental conditions means
426 that some reaches have experienced a more rapid terrestrialisation than others; thus reach
427 adjustment conditions along the river corridor must be taken into account to understand related
428 changes in biotic conditions. From a management perspective, these results underline the need to
429 take into account local environmental characteristics when developing restoration strategies based
430 on approaches at reach and corridor scales.

431 **4.2. Influence of multiple drivers on dike field forest structure and composition**

432 Overall, we found few differences in riparian forest attributes between pre-dam and post-
433 dam surfaces along the Rhône River. As such, differences were limited to greater dominance of
434 pioneer species on the younger post-dam dike fields and of post-pioneer and exotic species on the
435 older pre-dam ones. Beyond the expected successional patterns related to surface age (Janssen et
436 al., 2020), the high mean diameter values for pioneer species on post-dam surfaces and the
437 predominance of regeneration of post-pioneer species on pre-dam surfaces indicate widespread and
438 progressive stand aging. Regarding forest composition, only one species showed significant
439 differences in relative abundance between pre-dam and post-dam surfaces. This indicates that the

440 alteration of flow configuration and discharge regime due to dam commissioning, i.e., reduction of
441 average flow, frequency of high discharge and peak flows (Vázquez-Tarrío et al., 2019), did not
442 induce major changes in riparian forest attributes (e.g., strong mortality). One explanation beyond
443 this pattern may be related to the fact that major changes in environmental conditions within dike
444 fields (i.e., high accumulation of fine sediments and incision) occurred progressively over several
445 decades, after the initial channelization phase and prior to the dam construction period (Tena et al.,
446 2020). On the pre-dam surfaces, this allowed multiple possibilities for establishing succession but
447 also a gradual adaptation of the root systems to the new conditions. Conversely, on post-dam
448 surfaces the instantaneous and lasting dewatering induced by the diversion of flow in the canals left
449 few opportunities for the regeneration of pioneer species and led to the rapid development of stands
450 towards a post-pioneer phase.

451 Beyond the influence of channelization and flow regulation, related environmental variables
452 strongly shaped dike field forests. Specifically, we showed that the surface elevation best explained
453 changes in forest structure (Figure 5). Along the lateral dimension of the hydrosystem, hydrologic
454 aspects of the flood gradient strongly shape vegetation structure and composition (Naiman and
455 Decamps, 1997). Accordingly, a clear shift in forest composition was found between frequently
456 flooded surfaces, dominated by pioneer species (*Salix alba*), and non-flooded surfaces, dominated by
457 post-pioneer (*Juglans regia*, *Cornus sanguinea* and *Ligustrum vulgare*) and exotic species (*Acer*
458 *negundo* and *Robinia pseudoacacia*). Our results also indicate that the density and basal area of
459 exotic species, as compared to post-pioneer species, increased more with increasing surface
460 elevation (Catford et al., 2014). Although a high accumulation of fine sediments increases ecosystem
461 productivity by maintaining higher nutrient reserves (Franklin et al., 2009) and although resource-rich
462 environments promote exotic species (Nadal-Sala et al., 2017; Porté et al., 2011), our results show
463 that the position along the elevation gradient was of greater importance. Overall, this suggests that
464 sedimentation patterns within dike fields are rather homogeneous and that it is primarily differences
465 in elevation, and thus channel connectivity, which explain significant changes in species composition.

466 Finally, our results show limited effects of the reach position, as well as latitude, on riparian
467 forest structure. The main differences among the four reaches were related to greater density and
468 basal area of overstorey pioneer trees on the PDR reach and of exotic trees on the DZM reach. These
469 site-based differences are consistent with variation in environmental conditions amongst the sites. At
470 PDR the dike field surfaces were at lower elevation and potentially better connected to the water
471 table, which presumably maximize growing conditions for pioneer species. At the DZM site, the dike
472 field surfaces were highly disconnected due to higher sedimentation levels and potentially higher
473 nutrient pools, conditions which can favour invasion by more drought-tolerant exotic species (Nadal-
474 Sala et al., 2017; Porté et al., 2011). However, regarding riparian forest composition, a shift in species
475 pool was evidenced between the Continental northern and Mediterranean southern parts of the
476 river corridor. Among the native species, poplar dominance shifted in the downstream direction from
477 *Populus nigra* to *P. alba*. Exotic species also shifted, though between genera, from stands dominated
478 by *Acer negundo* in the north to *Robinia pseudoacacia* in the south. At all sites, some combination of
479 these two species dominated the understorey. These patterns suggest that the future of the Rhône
480 dike field forests will look very different from today and that the sustainability of local native
481 communities may be compromised through changes in biotic interactions and environmental
482 conditions (Vilà et al., 2011). Specifically, these two species may have different impacts on
483 biodiversity (Campagnaro et al., 2018), different management strategies (Merceron et al., 2016;
484 Vítková et al., 2020) and varying responses to ongoing global changes (Camenen et al., 2016).
485 Therefore, understanding the local-scale effect of climate *versus* human-induced stressors on
486 ecosystem properties is essential to designing effective restoration approaches along the entire
487 length of the river corridor. The shift in native and exotic species composition observed reinforces
488 the need to account for the climatic gradient to understand changes in vegetation dynamics, in order
489 to contextualize the impact of human stressors and thus adapt management strategies
490 appropriately.

491 **4.3. Characterizing the imprint of long-term human stressors on dike field riparian forests**

492 Nearly all riparian forest attributes and tree species varied significantly between dike-fields
493 and the more natural systems comprising young vegetation on recently-formed point bars and
494 mature forests on older floodplains. As expected, the density of small pioneer trees of the family
495 Salicaceae (*Populus* and *Salix* spp.) dominated the understory and overstorey of the young stands,
496 while regeneration of these species was almost absent in dike fields and in the mature forest.
497 Conversely, a few very large pioneer trees dominated the dike field stands, indicating a lack of flood
498 disturbance and subsequent regeneration on these surfaces (Vázquez-Tarrío et al., 2019), along with
499 an early maturation of these stands to their maximum potential biomass. Thus, despite large
500 variations in surface age among dike field sites (i.e., range 22-135 years), large pioneer trees already
501 dominated the youngest surfaces (Janssen et al., 2020), indicating high growth rates of Salicacea
502 species in these resource-rich environments (Karrenberg et al., 2002).

503 Compared to young and mature riparian forests, dike field forests were dominated by exotic
504 species, especially *Acer negundo*. Beyond the fact that several exotic species have been voluntarily
505 introduced for the needs of human activities in the Rhône catchment, such as *Robinia pseudoacacia*
506 and *Morus alba*, dike fields may be particularly susceptible to invasion because the modified
507 hydrologic and sedimentologic conditions decrease the recruitment niche for pioneer species as the
508 surfaces rapidly terrestrialize (Janssen et al., 2020; Kui et al., 2017). The disconnection of the dike
509 field surfaces from the river channel and the reduction in flood frequency and duration reduce the
510 creation of new fluvial landforms, diminish the substrate moisture regime, and limit the potential for
511 dispersal by hydrochory, all to the detriment of pioneer species (Nilsson et al., 2010). At the same
512 time, *Acer negundo* has been shown to be more resistant to a high rate of burial by fluvial sediments
513 (Kui and Stella, 2016), to establish more easily, through facilitation processes, in pioneer-dominated
514 stands (Saccone et al., 2010) and therefore to out-compete native pioneer species in resource-rich
515 environments (Porté et al., 2011). Moreover, once dense stands of *A. negundo* become established
516 on fluvial surfaces, their intense shade and high growth rates tend to preclude recruitment of
517 competitors, particularly shade-intolerant pioneer species. Overall, our results highlight that current

518 dike field forest structure and composition bear little resemblance to more natural areas, as no bank
519 erosion occurs, pioneer tree regeneration is rare and exotic tree species are highly represented.

520 Considering that the disconnection of dike field surfaces from the river channel is the main
521 factor driving changes in riparian forest attributes along the Rhône River, restoration actions that
522 increase this connection should be favoured at the reach scale. Indeed, river-wide restoration
523 strategies aiming to recreate a dynamic mosaic of changing habitats with patches of different ages,
524 as found on more natural alluvial rivers (e.g., Cooper et al., 2003; Johnson et al., 1976), would rely on
525 extremes interventions, such as wholesale removal of dams and dikes to re-establish historical flow
526 and sediment regimes. Given the unrealistic nature of this approach, we argue that restoration
527 actions should target local reaches where there is potential for improvement, seeking to restore the
528 natural physical and ecological processes that reconnect the river channel to its riparian margins. This
529 can be done by dismantling part of the dike fields, at least for their upper parts, in order to re-
530 establish bank erosion and recreate bare alluvial surfaces and a graduated floodplain and terrace
531 complex in the fluvial corridor of individual bypassed reaches. Bank re-erosion is a tricky process, not
532 so easy to re-establish in reaches where bed load transport is interrupted (Arnaud et al., 2015).
533 Moreover, groundwater may be also raised by increasing the minimum flow in the bypassed
534 channels, as was done in the 2000s for the restoration of aquatic habitats (Lamouroux et al., 2015) so
535 as to reinforce hydrological connectivity of floodplain. These measures can be especially effective in
536 favouring the regeneration of pioneer species that are most threatened along the Rhône River
537 corridor, especially along the less disconnected reaches, such as the Péage de Roussillon bypassed
538 reach.

539 Finally, the adaptation and persistence of exotic species to the human-altered hydro-
540 geomorphic environment of the Rhône corridor suggest that other interventions such as local
541 eradication or broader-scale floodplain clearing may be needed to simulate the natural processes of
542 floodplain development and native forest regeneration (Cooper and Andersen, 2012). Though these
543 actions may be effective in individual sites, they are likely impractical at the river corridor scale

544 because of the enormous costs involved and the uncertainty of the expected results. Therefore, we
545 argue that the restoration of severely degraded environments will require a nuanced mix of
546 approaches at different spatial scales (Bernhardt and Palmer, 2011). Along the Rhône River,
547 restoration operations should be prioritized first in reaches where restoration of physical process is
548 most likely to occur, mainly the longest ones where we can restore bedload transport and local bank
549 re-erosion. On other reaches with lower potential, however, it seems more appropriate to adapt
550 current forest stand management to local conditions by promoting the development of sustainable
551 habitats for biodiversity and improving the ecosystem services they provide.

552

553 **5. Conclusion**

554 Along the Rhône River margins, engineered modifications due to human infrastructure have
555 induced profound changes in both abiotic and biotic conditions within the riparian environment.
556 Compared to more natural riparian forests, we showed that channelization leads to a rapid
557 terrestrialsation of dike field surfaces, which steers stand development towards a new composition
558 and structure. As a secondary influence, flow regulation reinforces this effect. Given that current dike
559 field surfaces are no longer subject to erosion processes and that the return to a pre-disturbance
560 state at the corridor scale is very unlikely, pragmatic approaches should be favoured to maximize
561 ecological values given the current state (Dufour and Piégay, 2009). In this view and in accordance
562 with Thorel al. (2018), we argue that the ecological and sociological cost-benefit of restoration
563 actions should be better evaluated. Therefore, we believe that a process-based restoration strategy
564 should be implemented by giving priority to bypassed reaches with the greatest ecological potential
565 (e.g., by facilitating the regeneration of pioneer species on surfaces with lower elevation) through
566 bed load transport restoration coupled with bank re-erosion. On other bypassed reaches,
567 management of dike field forests could aim to improve the ecological benefits provided by these
568 human-made ecosystems in terms of suitable habitat for biodiversity (e.g. in-channel wood, large
569 living trees and related microhabitats) as well as other services (e.g., recreational areas, pollutant

570 mitigation and carbon storage). We believe that implementing a hierarchical, multiscale approach
571 based on local reach conditions and species pools will maximize the ecological benefits of restoration
572 actions along the Rhône River corridor. Given that channelization and flow/bed load regulation are
573 among the most common human interventions in rivers that constrain the dynamics of riparian
574 communities, these results for the dike field forests along the Rhône River should be readily
575 transferable to other human-altered riparian ecosystems.

576

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589

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809

810 **Table 1.** Top-ranking models predicting variations in understorey and overstorey riparian forest
811 attributes on dike fields along the Rhône River, SE France, as assessed with Akaike's information
812 criterion corrected for small sample size (AICc). The number of parameters estimated (k), AICc, AICc
813 weight (W) and adjusted coefficient of determination (R^2) are provided (see Appendix 8 for detailed
814 results of all candidate models).

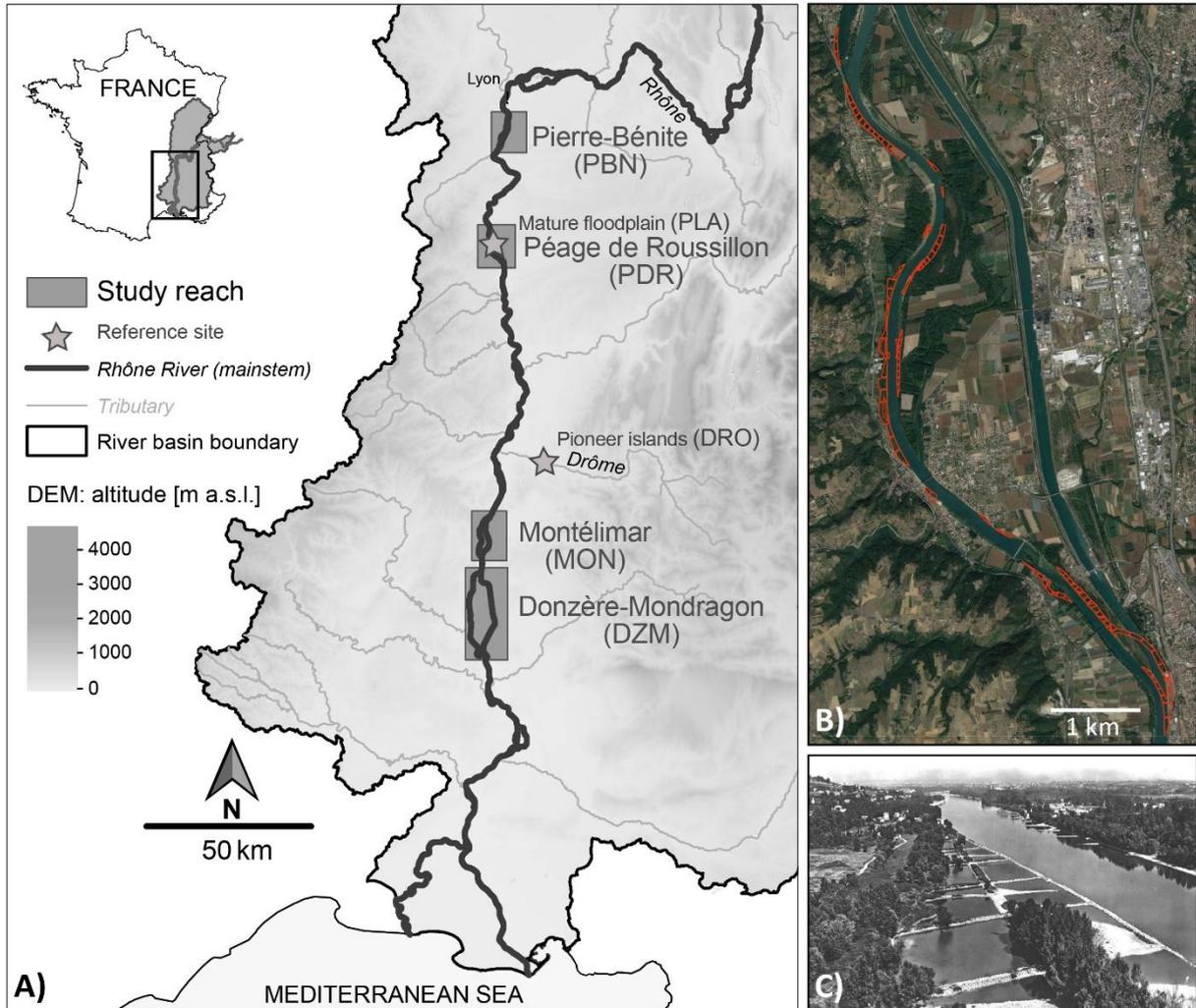
	Variable	Top-ranked model	AICc	W	R^2	
Understorey	Stem density (n ha ⁻¹)	- Pioneer	Fine sediment depth	333.5	0.531	0.053
		- Post-pioneer	Surface elevation	370.2	0.475	0.088
		- Exotic	Surface age	406.8	0.286	0.028
	Basal area (m ² ha ⁻¹)	- Pioneer	Fine sediment depth	-8.2	0.494	0.046
		- Post-pioneer	Surface elevation	185.1	0.530	0.147
		- Exotic	Latitude	137.4	0.768	0.082
	Mean	- Pioneer	Null	8.3	0.525	0.000
	diameter (cm)	- Post-pioneer	Inundation duration	77.0	0.329	0.037
		- Exotic	Surface elevation	72.8	0.655	0.124
Overstorey	Stem density (n ha ⁻¹)	- Pioneer	Surface elevation	267.9	0.558	0.104
		- Post-pioneer	Surface elevation	292.0	0.398	0.084
		- Exotic	Surface elevation	254.6	0.916	0.266
	Basal area (m ² ha ⁻¹)	- Pioneer	Surface elevation	209.4	0.771	0.130
		- Post-pioneer	Surface age	158.6	0.530	0.078
		- Exotic	Surface elevation	166.5	0.999	0.426
	Mean	- Pioneer	Inundation duration	71.7	0.258	0.018
	diameter (cm)	- Post-pioneer	Null	53.8	0.292	0.000
		- Exotic	Surface elevation	49.0	0.405	0.088

815

816 **Figure 1.** Location of the four bypassed reaches studied along the Rhône River in southeastern France

817 (A), distribution of the dike fields in the Péage de Roussillon bypassed reach (B, aerial photographs:

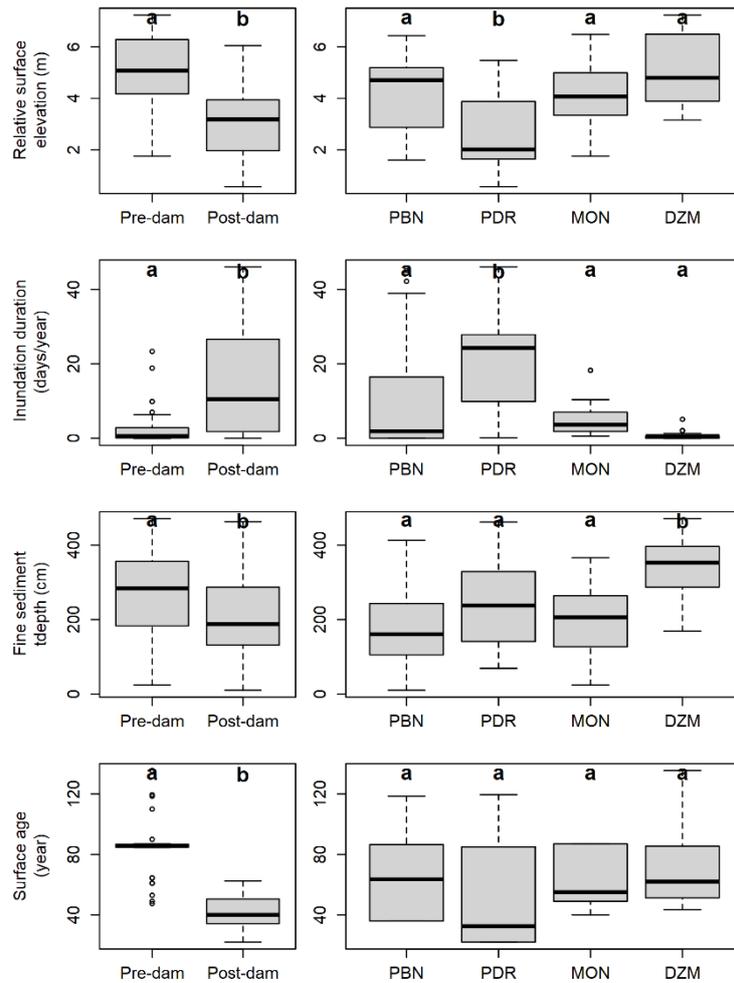
818 Google Map) and detailed view of the dike fields early in the 20th century, before terrestrialization



819 and afforestation (C, postcard: SMIRIL).

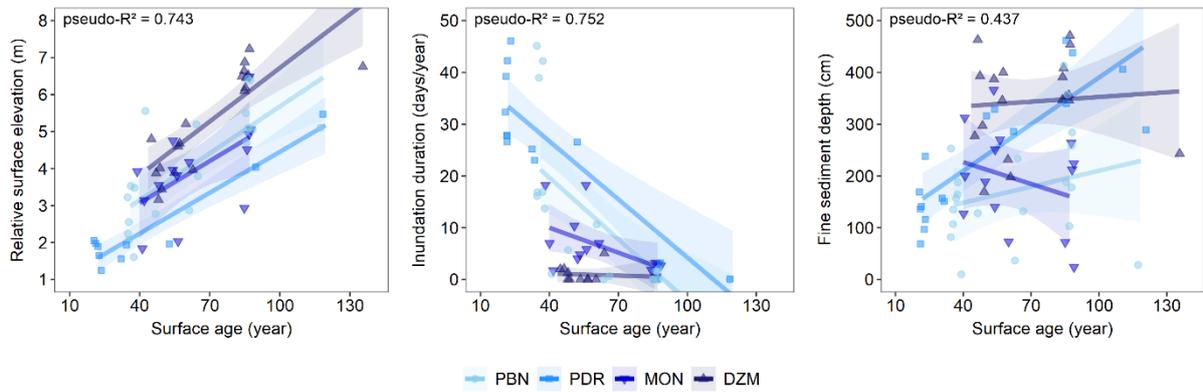
820

821 **Figure 2.** Variation in environmental variables between pre- and post-dam surfaces and bypassed
 822 reaches (PBN = Pierre-Bénite, PDR = Péage de Roussillon, MON = Montélimar, DZM = Donzère-
 823 Mondragon) on dike fields along the Rhône River, SE France. Boxplot with different letters indicate
 824 statistical significant differences ($p < 0.05$) among factor levels, based on one-way ANOVA's and
 825 Tukey's post hoc tests (see
 826 Appendix 5 for details).

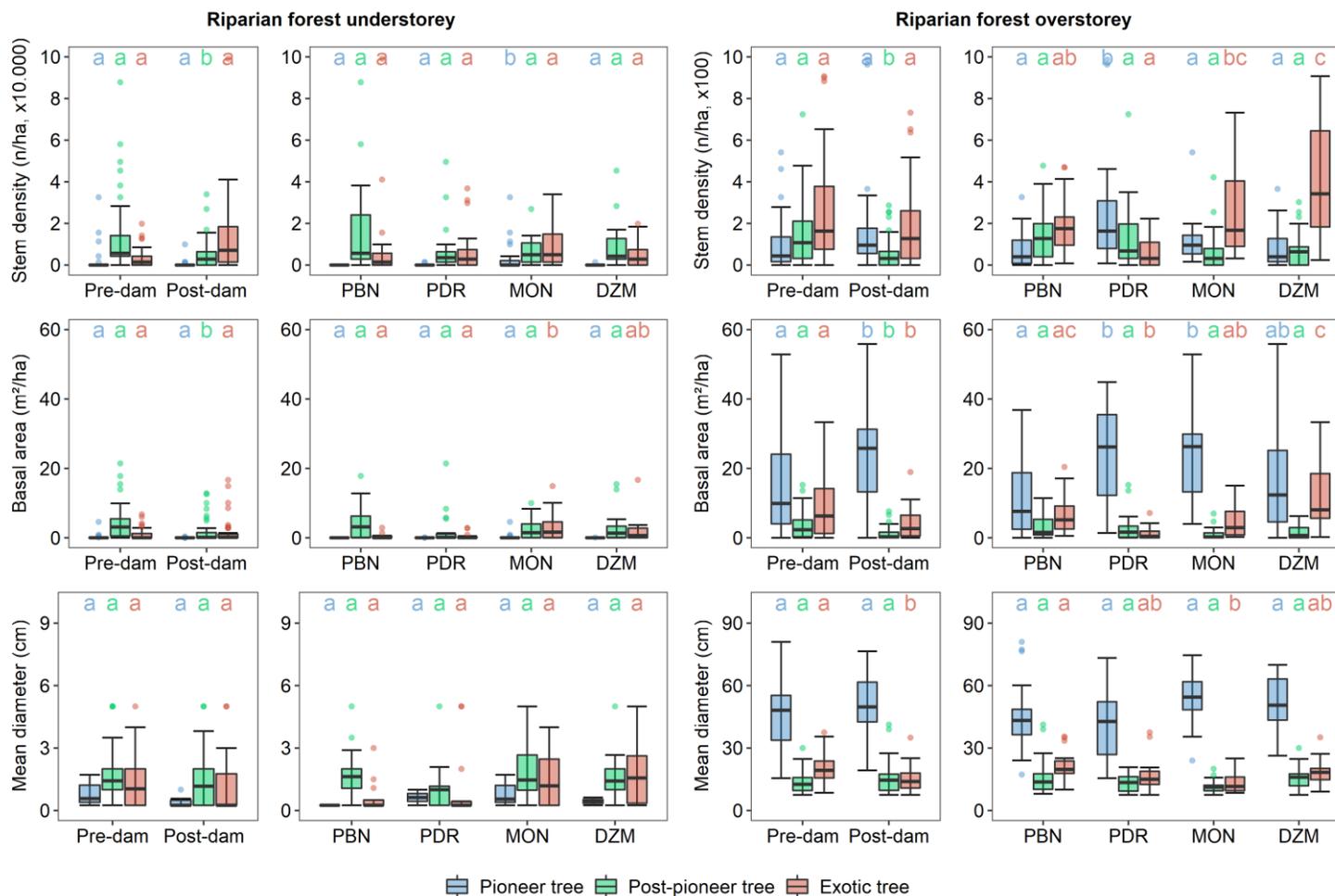


827 **Figure 3.** Variation in relative surface elevation , inundation duration and fine sediment depth at
828 dike-field forest sites as a function of surface age along the Pierre-Bénite (PBN), Péage de Roussillon
829 (PDR), Montélimar (MON) and Donzère-Mondragon (DZM) bypassed reaches of the Rhône River, SE
830 France (see Appendix 6 for details).

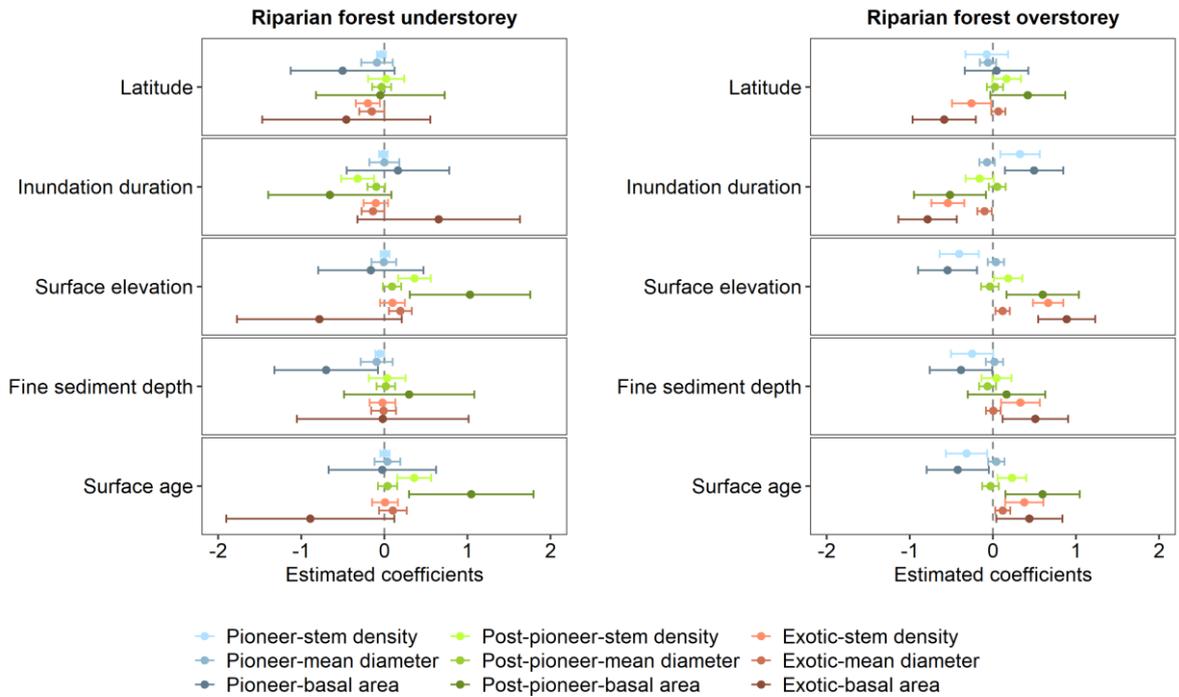
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832 **Figure 4.** Variations in understory and overstorey riparian forest attributes between pre- and post-dam surfaces and bypassed reaches (PBN = Pierre-Bénite,
 833 PDR = Péage de Roussillon, MON = Montélimar, DZM = Donzère-Mondragon) on dike fields along the Rhône River, SE France. Bars with different letters indicate
 834 statistical significant differences ($p < 0.05$) among factor levels, based on one-way ANOVA's and Tukey's post hoc tests (see Appendix 7 for details).

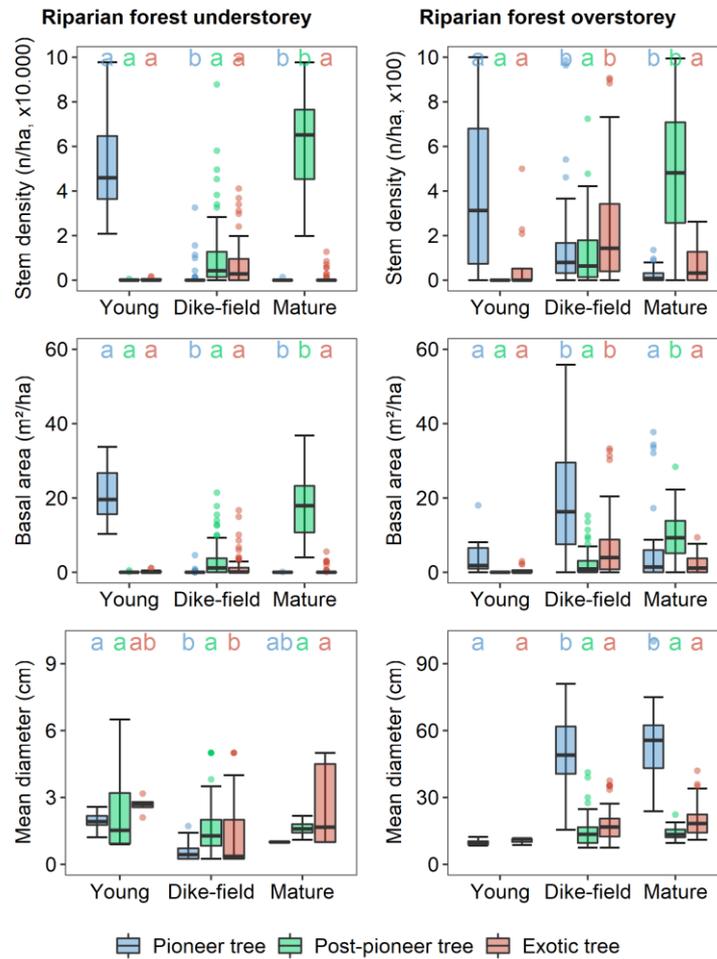


835 **Figure 5.** Average parameter estimates and 95% confidence intervals for environmental variables
 836 used to predict variations in understory and overstorey riparian forest attributes on dike fields along
 837 the Rhône River, SE France (full model results are listed in Appendix 8 and detailed results appear in



838 Appendix 9).

839 **Figure 6.** Variations in understory and overstorey riparian forest attributes between young
 840 vegetation stage, dike fields and mature vegetation stage, along the Rhône and Drôme rivers, SE
 841 France. Bars with different letters indicate statistical significant differences ($p < 0.05$) among factor
 842 levels, based on Tukey's post hoc tests (see Appendix 10 for details).



843 **Figure 7.** Constrained canonical analysis of principal coordinates (CAP) of riparian forest composition in relation to three contrasts: A) pre- vs post-dam surfaces
844 and bypassed reaches (PBN = Pierre-Bénite, PDR = Péage de Roussillon, MON = Montélimar, DZM = Donzère-Mondragon); B) environmental variables within
845 dike fields (relative surface elevation, inundation duration, surface age, fine sediments depth and latitude); and C) three stages of development of riparian
846 forests along the Drôme (young vegetation stage) and Rhône rivers (dike fields and mature vegetation stage), SE France. In panel C, the young and mature
847 riparian forests are more natural systems from the same bioregion to compare to dike field sites. To facilitate graphical interpretation, the centroids in principle
848 coordinate space are indicated for the 10 most influential tree species: Ace_neg = *Acer negundo*, Cor_san = *Cornus sanguinea*, Cra_mon = *Crataegus*
849 *monogyna*, Euo_eur = *Euonymus europaeus*, Fra_ang = *Fraxinus angustifolia*, Jug_reg = *Juglans regia*, Lig_vul = *Ligustrum vulgare*, Pop_alb = *Populus alba*,
850 Pru_fru = *Prunus x fruticans*, Rob_pse = *Robinia pseudoacacia*, Sal_alb = *Salix alba*, Sal_ele = *Salix eleagnos*, Sal_pur = *Salix purpurea*, Sam_nig = *Sambucus nigra*
851 (see also Appendices 11, 12 and 13).

