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## **Divergence of riparian forest composition and functional traits from natural succession along a degraded river with multiple stressor legacies**

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1 **Divergence of riparian forest composition and functional traits from natural succession along a degraded**  
2 **river with multiple stressor legacies**

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23

24 Running head: Accelerated succession on degraded river

25 **Abstract**

26 Prolonged exposure to human induced-stressors can profoundly modify the natural trajectory of ecosystems.  
27 Predicting how ecosystems respond under stress requires understanding how physical and biological properties  
28 of degraded systems parallel or deviate over time from those of near-natural systems. Utilizing comprehensive  
29 forest inventory datasets, we used a paired chronosequence modelling approach to test the effects of long-  
30 term channelization and flow regulation of a large river on changes in abiotic conditions and related riparian  
31 forest attributes across a range of successional phases. By comparing ecological trajectories between the highly  
32 degraded Rhône and the relatively unmodified Drôme rivers, we demonstrated a rapid, strong and likely  
33 irreversible divergence in forest succession between the two rivers. The vast majority of metrics measuring life  
34 history traits, stand structure, and community composition varied with stand age but diverged significantly  
35 between rivers, concurrent with large differences in hydrologic and geomorphic trajectories. Channelization  
36 and flow regulation induced a more rapid terrestrialization of the river channel margins along the Rhône River  
37 and accelerated change in stand attributes, from pioneer-dominated stands to a mature successional phase  
38 dominated by non-native species. Relative to the Drôme, dispersion of trait values was higher in young forest  
39 stands along the Rhône, indicating a rapid assembly of functionally different species and an accelerated  
40 transition to post-pioneer communities. This study demonstrated that human modifications to the hydro-  
41 geomorphic regime have induced acute and sustained changes in environmental conditions, therefore altering  
42 the structure and composition of riparian forests. The speed, strength and persistence of the changes suggest  
43 that the Rhône River floodplain forests have strongly diverged from natural systems under persistent multiple  
44 stressors during the past two centuries. These results reinforce the importance of considering historical  
45 changes in environmental conditions to determine ecological trajectories in riparian ecosystems, as has been  
46 shown for old fields and other successional contexts.

47

48 Key-words: riparian forests, ecological succession, community-weighted traits, human induced-stressors,  
49 ecological trajectories

## 50 **Introduction**

51           The concept of ecological succession dates almost to the origins of the field of ecology itself. Over the  
52 last century, conceptual frameworks of how plant communities assemble (or re-assemble) following large  
53 perturbations have evolved from a focus on pattern to the underlying mechanisms, notably the feedbacks that  
54 occur between abiotic and biotic ecosystem components as they develop over time (Connell and Slatyer 1977,  
55 Pickett et al. 1987, Meiners et al. 2015). This shift in focus has come with an increasing appreciation of  
56 ecological complexity, particularly the effects of multiple interacting drivers and stressors, thresholds and other  
57 non-linear responses, and the importance of contingent factors (e.g., variation in historical management  
58 strategies or in the intensity and duration of management) in driving community trajectories (Clark et al. 2019,  
59 Chang and Turner 2019). Nevertheless, synthesizing general principles and testing predictions of ecological  
60 succession across diverse ecosystems remain a challenge. The recent focus on monitoring change in ecological  
61 traits, rather than species composition, in plant assemblages over time shows promise in distilling patterns and  
62 drivers of community dynamics in response to shifts in both extrinsic factors (e.g., disturbance, climate) and  
63 intrinsic ones (e.g., soil properties, competition) (Meiners et al. 2015, Chang and Turner 2019).

64           The trait-based approach is particularly well-suited for studying natural communities that are severely  
65 degraded by multiple, interacting human stressors; these include resource exploitation (e.g., overfishing),  
66 exotic species invasions, and changes in land use, climate and disturbance regimes due to human activities  
67 (Mouillot et al. 2013). As with natural disturbances, human-induced stressors can greatly alter ecological  
68 trajectories of both terrestrial and aquatic ecosystems, and lead to rapid and potentially irreversible shifts in  
69 ecosystems properties (Folke et al. 2004). Numerous studies document divergences in successional trajectories  
70 of species assemblages and functional traits between altered and reference ecosystems (e.g., Odion et al. 2010,  
71 Sfair et al. 2016, Clark et al. 2019), in many cases leading to alternative ecosystem states (Beisner et al. 2003).  
72 Strong shifts in species dominance during succession due to native biodiversity loss and/or invasion by exotic  
73 species may impede the ecological resilience of ecosystems, and compromise efforts to restore them or  
74 preserve their functions and services (Suding 2011).

75           Riparian ecosystems are among the most modified by human activities (Tonkin et al. 2018) and  
76 comprise some of the most vulnerable biomes to ongoing global change (Perry et al. 2012, Stella et al. 2013b).  
77 More than most forest ecosystems, riparian woodlands comprise a fragmented patch mosaic of diverse  
78 composition and age, which are related to strong physical gradients and flood history (Naiman and Decamps

79 1997, Scott et al. 1997, Bendix and Stella 2013). Abiotic conditions and plant species composition can change  
80 markedly within only a few decades during riparian succession (Johnson et al. 1976, Osterkamp and Hupp  
81 2010), and community trajectories can be interrupted and superimposed by new disturbances. Nevertheless,  
82 riparian disturbance regimes present an excellent opportunity to study succession at local scale. Frequent flood  
83 disturbance and the close proximity of forest stands that have colonized floodplain surfaces of different ages  
84 allow the use of chronosequences, or space-for-time proxies, to study successional processes in riparian  
85 communities (Stella et al. in review, Schnitzler 1995, Scott et al. 1997, Fierke and Kauffman 2005). In the  
86 absence of long-term longitudinal datasets, which with few exceptions are virtually absent for riparian areas  
87 (but see the case of the Missouri River, USA in Johnson et al. 2012), this approach is particularly suited to  
88 understand how community dynamics along highly modified rivers may diverge from historical or reference  
89 conditions (Prach and Walker 2011).

90 To date, the effect of human induced-modifications on riparian communities have mostly been studied  
91 by adopting a comparative approach. By comparing channelized versus unchannelized rivers (Dufour, Barsoum,  
92 Muller, & Piégay, 2007; Nakamura, Jitsu, Kameyama, & Mizugaki, 2002; Oswalt & King, 2005) or regulated  
93 versus unregulated rivers (Merritt and Cooper 2000, Kui et al. 2017, Bejarano et al. 2018), negative impacts to  
94 riparian communities have been documented, including reduced native species and functional trait diversity,  
95 increased invasion by exotic species, and homogenised forest stand structure. Despite widespread degradation  
96 to riparian systems and the substantial investigations into the ecological mechanisms that drive succession  
97 (Chang and Turner 2019), few studies have examined how modifications to river flow and sediment regimes  
98 impact the successional trajectory of riparian plant communities, and none to our knowledge have analysed  
99 these patterns in terms of functional trait dynamics. Yet, understanding both the current status and future  
100 trajectory of degraded riparian forest ecosystems is critical for defining and prioritizing effective strategies to  
101 conserve and restore them.

102 In this context, we aimed to understand how the current ecological trajectory of riparian forests along  
103 a large, channelized and regulated river in eastern France either paralleled or deviated from a relatively  
104 unmodified local reference system, across a range of successional phases. Using datasets of abiotic drivers –  
105 flow and sediment regimes – and biotic responses that included functional, structural and compositional  
106 attributes, we modeled chronosequences on both rivers to test for deviation in their ecological trajectories.  
107 The chronosequence approach is well-suited for assessing community shifts during plant succession, especially

108 if these changes are predictable over time (Walker et al. 2010). Moreover, comparing trends in species and  
109 trait composition over time can help to identify the mechanisms causing divergence in ecological trajectories,  
110 and thus potential barriers to restoration (Suding 2011, Chang and Turner 2019). Based on this scheme we  
111 addressed the following two questions: (i) How do abiotic and biotic conditions vary with forest stand age along  
112 a heavily impacted river compared to a more natural reference ecosystem? (ii) Are successional trajectories of  
113 riparian forests different between both river systems, in terms of species composition and functional trait  
114 trends over a long chronosequence?

115

## 116 **Materials and methods**

### 117 **Study area**

118 The study was carried out along the mainstem Rhône River (total length = 810 km, catchment area =  
119 96,500 km<sup>2</sup>, mean annual discharge = 1,700 m<sup>3</sup> s<sup>-1</sup>) and the Drôme River (total length = 110 km, catchment area  
120 = 1,663 km<sup>2</sup>, mean annual discharge = 20 m<sup>3</sup> s<sup>-1</sup>), a tributary of the Rhône (Figure 1). Both rivers are located in  
121 SE France and experience a temperate climate with mean annual temperature and precipitation of 13.6°C and  
122 755 mm in the southern part and of 11.9°C and 782 mm in the northern part. Despite differences in catchment  
123 size and discharge magnitude, the rivers prior to human modification shared similar snowmelt flow regimes  
124 and sediment dynamics. The riparian forests of both rivers contain a mix of early successional trees including  
125 *Populus nigra* and *Salix alba*, post-pioneers such as *Fraxinus excelsior* and *Acer platanoides*, and understorey  
126 species including *Crataegus monogyna* and *Sambucus nigra*. The most abundant newcomers to the species  
127 pool include the non-native trees *Acer negundo* and *Robinia pseudoacacia* (See Appendix S1 for further details  
128 on tree species' characteristics).

129 The Drôme River is a free-flowing river with a channel mostly unconstrained by human infrastructure  
130 and a shifting braided pattern throughout its downstream portion, which constitutes the study reach. Bedload  
131 is still actively transported in the lower section despite channel incision due to sediment mining that occurred  
132 during the 1970s. Since the second half of the 20<sup>th</sup> century, the Drôme River has also been subject to land-use  
133 changes in the floodplain (Liébault and Piégay 2002). Both mining and land-use changes have favored  
134 establishment of native riparian woodlands within the braided section, which is subject to periodic floods that  
135 scour older forest patches and induce sediment deposition and subsequent initiation of new stands. As a

136 consequence, the riparian forest is characterized by a complex mosaic of patches of different ages (Räpple et  
137 al. 2017).

138 The lower Rhône River, downstream of the city of Lyon, is a highly modified river, which has shifted  
139 from a braided pattern to a series of impounded reaches within the span of approximately one century  
140 (Olivier et al. 2009, Bravard 2010). Two main historical management phases have greatly modified the river  
141 during this period. During the 19<sup>th</sup> Century the river was engineered and channelized of longitudinal  
142 submersible dikes and lateral dikes, forming more or less rectangular compartments, called “casiers Girardon”  
143 (see 1954 photo in Figure 1). These structures were constructed within the river’s main channel and arranged  
144 sequentially along extensive reaches of the river to concentrate flow into a single narrow channel, thus  
145 facilitating navigation (see Thorel et al. 2018 for further details). In the second management phase, nineteen  
146 hydropower plants were built along the French part of the Rhône River during the second half of the 20<sup>th</sup>  
147 Century, among which sixteen plants were built on artificial channels that bypass 162 km out of 522 km of the  
148 river (Lamouroux et al. 2015). Each of these hydropower works contains a diversion dam that impounds a  
149 reservoir upstream and conveys a large part of the river discharge into the diversion canal on which the power  
150 plant is located for energy production (for further details see, Appendix S2 and Vázquez-Tarrío et al. 2019). As a  
151 consequence, the historical bypassed channels, also called the old Rhône, receives a minimum discharge most  
152 of the year, on average 5% of the natural discharge (Bravard and Gaydou 2015). Thus, these bypassed channels  
153 which had been previously channelized are also significantly impacted by river regulation, which have induce  
154 channel incision, lateral stabilization and armouring of the channel bed. Along the highly artificial, stable river  
155 margins of the bypassed channels, many of the Girardon structures filled with overbank fine sediment and  
156 were subsequently colonized by woody pioneer species and succeeded to mature riparian forests (Räpple  
157 2018).

#### 158 **Riparian forest inventory sampling design**

159 Forest inventories were conducted along both the Drôme and Rhône rivers and confined to  
160 established stands in the active and abandoned floodplain of each river. To ensure independence and avoid  
161 edge influences, all inventory plots were established > 60 m away from any other plot, were located in forested  
162 patches > 0.5 ha and were > 20 m from the nearest stand edge. Along the Drôme River, 69 plots were sampled  
163 in the summer of 1994 within the Natural Reserve of the Ramières, in which large patches of riparian forest  
164 remain. The plots were distributed between two braided reaches, west (n = 19 plots) and east (n = 50)

165 (Appendix S3). Along the Rhône River, 65 plots were surveyed along four bypassed channels (*i.e.*, the former  
166 active channel) in summer 2015. From upstream to downstream, these reaches were: Pierre-Bénite (PBN, n =  
167 16 plots), Péage de Roussillon (PDR, n = 14), Montélimar (MON, n = 18) and Donzère-Mondragon (DZM, n = 17)  
168 (Appendix S3). Currently, the Girardon structures in these four bypassed channels support the largest extent of  
169 riparian forests remaining along the lower Rhône River downstream of Lyon.

170 On the Drôme River, stands were characterized using a 13.8-m-radius circular plot (area: 597 m<sup>2</sup>),  
171 centered on a systematic 130 x 130 m grid covering the whole forest area of the Natural Reserve. Within each  
172 plot, all standing trees with a diameter at breast height (DBH) ≥ 7.5 cm were recorded. On the Rhône River, a  
173 stratified sampling scheme was implemented, with plots randomly located within floodplain areas of known  
174 age. Rhône inventories used two concentric plot sizes, with a 10-m radius plot (area: 314 m<sup>2</sup>) for recording  
175 standing trees with a DBH ≥ 7.5 cm, and a larger plot of 20-m radius (area: 1,256 m<sup>2</sup>) used to record standing  
176 trees with DBH ≥ 30 cm. For each tree, species, DBH and health class were recorded, comprising live trees (<  
177 50% dead crown and branches), dying trees (>50% dead crown and branches), or dead trees.

178 To accurately compare stand attributes between the two rivers, which were subject to different forest  
179 inventory campaigns, data were standardized to a per hectare basis and common metrics in both systems  
180 describing riparian forest composition and structure were used (Table 1). Basal area (m<sup>2</sup> ha<sup>-1</sup>), mean diameter  
181 (cm) and stem density (n ha<sup>-1</sup>) were calculated for total live and total dead standing trees, as well as subsets for  
182 total exotic trees, and standing live trees of several genera: *Populus* spp. (*i.e.*, *P. alba*, *P. x canescens*, *P. nigra*,  
183 *P. tremula* and *P. x canadensis*), *Fraxinus* spp. (*i.e.*, *F. angustifolia* and *F. excelsior*) and *Acer* spp. (*i.e.*, *A.*  
184 *campestre*, *A. monspessulanum*, *A. negundo*, *A. opalus*, *A. platanoides* and *A. pseudoplatanus*). Diversity  
185 metrics of tree diameter classes (5-cm ranges across n = 14 classes) and tree species (n = 31) were computed  
186 using the Shannon diversity index with integer values of basal area as the abundance weighting measure.

187 Overbank fine sediment depth was measured at the center of each plot using a soil corer that was  
188 inserted into the fine sediment until the gravel interface was reached (Table 1). Mean and standard-deviation  
189 of annual flow were calculated using daily data recorded between 1966 and 2017 for the Drôme River  
190 (<http://hydro.eaufrance.fr>) and between 1920 and 2010 for the Rhône River (provided by the Compagnie  
191 Nationale du Rhône). Because forest inventories on the two rivers were conducted in different periods (*i.e.*,  
192 Drôme = 1994, Rhône = 2015), we used a common time frame, fixed between 1940 and 2000, to compare  
193 changes in hydrology but also to account for different switch-on dates of the diversion canals along the Rhône



194 River (i.e., DZM = 1952, MON = 1957, PBN = 1966, PDR = 1977). We used data from the Saillans measurement  
195 station on the Drôme River, 15 km upstream of the east sampling area, and from two stations on Rhône River,  
196 at Ternay within the PBN bypassed channel, and at Viviers within the MON bypassed channel. These two  
197 stations' data were then averaged to estimate unregulated flow prior to the diversions in each reach, whereas  
198 regulated flow levels were estimated using dam operation rules imposed following the diversions.

#### 199 **Trait data**

200 Exotic tree species were distinguished from native tree species, using data available from the Baseflor  
201 database (Julve 1998). For functional traits, we focused on three traits that typically vary across different life  
202 history strategies as plants response to shifts in limiting resources and competitors during ecological  
203 succession: specific leaf area (SLA; leaf area per dry mass), wood density, and dry seed mass. SLA is related to  
204 resource acquisition and conservation strategies, contrasting "conservative" species with long-lived leaves to  
205 "acquisitive" species with rapid turnover of plant leaves (Wright et al. 2004). Wood density is related to growth  
206 strategy, contrasting fast-growing species with low wood density against slow-growing but stress-tolerant  
207 species with high wood density (Chave et al. 2009). Seed mass is related to dispersal ability, contrasting species  
208 with light seeds but high seedling mortality from species with large seeds but high long-term seedling survival  
209 (Westoby 1998). In riparian environments, where large and rapid changes in abiotic stressors and available  
210 resources drive community dynamics, this set of traits is expected to vary greatly among tree species and with  
211 forest stand age. Due to contrasting life-history strategies between pioneer and post-pioneer riparian species,  
212 we expected to see increasing trends across young to old forest stands in community weighted averages of SLA  
213 (from rapid to longer leaf turnover), wood density (from faster to slower growth) and seed mass (from long-  
214 distance to more local dispersal).

215 Trait data were extracted from the TRY database, from which we calculated a mean trait value per  
216 species, after removing all values with an error risk > 4 (Kattge et al. 2011, see Appendix S4). Missing values in  
217 the wood density data were completed using the global wood density database (Zanne et al. 2009, Chave et al.  
218 2009). For each trait value, we computed community-weighted means (CWM) and functional dispersion (FDis)  
219 using basal area as a measure of relative abundance. CWM is defined as the mean of trait values weighted by  
220 the relative abundance of each species bearing each value (Lavorel et al. 2008). FDis is defined as the mean  
221 distance of individual species to the weighted centroid of all species in the assemblage and is unaffected by  
222 difference in species richness among plots (Laliberté and Legendre, 2010).

## 223 **Forest stand age reconstruction**

224 Forest stand age was characterized using geo-referenced aerial photograph series in a Geographic  
225 Information System (QGIS Development Team 2015). For the Drôme River, seven series of aerial photographs  
226 were available, taken from 1932 to 1991. For the Rhône River, available information varied among reaches and  
227 among plot positions within reach, with four to six series of aerial photographs available per reach, taken from  
228 1938 to 2002 (see Appendix S3 for details). For each plot, the physiognomic unit was characterized visually  
229 from aerial photographs into four categories: water, bare ground, shrub (*i.e.*, sparse patches of low vegetation)  
230 and forest units (*i.e.*, dense patches of tall vegetation). The effective timing of forest establishment for each  
231 plot was determined by averaging the last unforested series date ( $t = \text{no forest cover}$ ) and the next one where  
232 forest was evident ( $t+x = \text{forest cover}$ ). When a time-series was too fragmented, *i.e.*, > 20 years between two  
233 superimposed aerial photographs, and when physiognomic units were “shrubs” on the old aerial photograph  
234 series and “forest” on the next series, the date of forest cover was approximated in between the two dates. To  
235 confirm the continuity of the forest cover since the first date of appearance, posterior aerial photograph series  
236 were also inspected (Appendix S3).

## 237 **Statistical analysis**

238 We used linear models to test how abiotic drivers and biotic responses varied across the forest stand  
239 age (or years), and whether these trends differed significantly between rivers. For all models, we considered  
240 forest stand age (“Age” in tables and figures) as a continuous predictor, as well as sediment depth  
241 (“Sed\_depth”). Both of these variables were standardized prior to analysis. River (noted “River”) was  
242 considered as an independent, categorical factor. Abiotic drivers included the fine sediment depth as well as  
243 the mean and standard deviation (SD) of annual flow. Because the discharge was largely different between the  
244 two rivers, mean and SD of annual flow were standardized according to the range of their own values prior to  
245 analysis. Biotic response included the community-weighted mean (CWM) and the dispersion (FDis) of  
246 functional trait values, the basal area, the mean diameter and the stem density of stand attributes and of tree  
247 genera as well as the diversity indices (Table 1). Because the seed mass of two tree species – *Juglans regia* and  
248 *Quercus pubescens* – was very large, seed mass values were log-transformed before CWM and FDis calculation.

249 To investigate how abiotic drivers and biotic responses varied over time between the two rivers, we  
250 fitted normal linear models (LMs) or log-normal LMs for skewed response variables (*i.e.*, sediment depth, SLA,  
251 wood density, basal area, diameter and stem density). We developed a set of *a priori* models testing the

252 individual, additive and interactive effects of predictor variables, plus a null (*i.e.*, intercept-only) model (see  
253 Appendices S5 and S6). In all candidate models the variance inflation factor was < 3. The most parsimonious  
254 model was identified using Akaike's information criterion corrected for small sample sizes (Burnham and  
255 Anderson 2002) and goodness of fit was estimated using the adjusted coefficient of determination. For all of  
256 the response variables, Moran's I values in the top-ranked model residuals was non-significant, indicating that  
257 spatial patterns were accounted for by independent variables (Appendix S7). For each response variable,  
258 parameter estimates and associated unconditional standard errors were extracted from the top-ranked model  
259 and we checked for consistency among parameter estimates and confidence intervals on the subset of top  
260 ranking models for which the delta AICc was < 7 (Appendix S5 and S6).

261 To investigate whether the forest structure and composition varied with forest stand age between the  
262 two rivers we used multivariate generalized linear models (GLMs). We fitted the full model (Age x River +  
263 Sed\_depth) to each diameter class/tree species, using basal area as the abundance measure, and summed  
264 across the univariate responses to estimate their multivariate response with a negative binomial distribution.  
265 The significance of independent variables in the multivariate GLM was assessed using an analysis of variance  
266 with the PIT-trap method and 999 bootstrap resamples (Warton et al. 2017). To determine which diameter  
267 classes/tree species best contribute to the overall model deviation, we calculated univariate test statistics and  
268 p-values, and adjusted to correct for multiple testing for each diameter classes and tree species (Wang et al.  
269 2012). Finally, to provide a graphical representation of the interaction between forest stand age and river, we  
270 used a canonical analysis of principal coordinates (Anderson and Willis 2003), using a Bray-Curtis distance. All  
271 analyses were performed with R version 3.5.3. (R Core Team 2019).

272

## 273 **Results**

### 274 **Contrasting trends in abiotic drivers among rivers**

275 Of the abiotic drivers analysed, sediment depth and mean annual flow had pronounced trends over  
276 time that differed significantly between the Rhône and Drôme rivers (Table 2; Figure 2). Thus, models that  
277 included an interaction term between river and forest stand age (for sediment depth) or river and year (for  
278 mean discharge) best predicted the respective response. Sediment depth increased more rapidly with forest  
279 stand age along the Rhône compared to the Drôme (Figure 2), whereas the mean annual flow strongly  
280 decreased over time along the Rhône, with no clear trend on the Drôme (Appendix S8). The standard-deviation

281 of annual flow decreased significantly over time (Figure 2) but did not differ significantly between the two  
282 rivers (Appendix S8).

### 283 **Trends in forest functional, structural and compositional attributes**

284 Most of the whole-stand and genera-specific forest attributes, community-weighted functional traits,  
285 and diversity indices varied strongly with riparian forest stand age. Similar to the abiotic drivers, many of the  
286 trends in forest development also differed significantly between rivers. For a large fraction of the response  
287 variables, the top-ranked model included the interaction term between stand age and river, and some of these  
288 included sediment depth as a covariate (Table 2). The goodness of fit of these models ranged greatly, from 0.08  
289 for the basal area of *Populus spp.*, to 0.71 for the mean diameter of *Populus spp.* (Table 2).

290 Parameters retained in the top ranked models indicate that only a few trends in forest characteristics  
291 were equivalent between rivers; these were overall mean seed mass, and for *Fraxinus spp.* only, their basal  
292 area and stem density (Table 3). Some characteristics varied at the same rate (i.e., parallel slopes for both  
293 rivers), but differed significantly in magnitude between the Drôme and Rhône. These included stem density for  
294 live and dead trees, which were consistently higher along the Drôme River. In contrast, stem density and mean  
295 tree diameter for exotic trees, mean tree diameter for *Fraxinus spp.* and *Acer spp.*, as well as functional  
296 dispersion of SLA were significantly higher along the Rhône River (Table 1; Figure 3 and 4).

297 All others trait and stand-level responses were mediated by the interaction terms between river and  
298 forest stand age (Tables 3). For example, the mean value for SLA and wood density (Figure 3), and the basal  
299 area of exotic trees (Figure 4) increased more steeply with forest stand age along the Rhône River. Conversely,  
300 the Drôme River riparian forest showed steeper trends over time for the trait dispersion of wood density and  
301 seed mass (Figure 3), *Acer spp.* basal area and stem density (Figure 5), as well as the diversity of tree species  
302 and of stem diameter classes (Figure 6). For some responses, the two rivers showed opposite trends. In  
303 particular, the basal area and mean diameter of live and dead trees (Figure 4), as well as the basal area of  
304 native *Populus spp.* (Figure 5), increased with forest stand age along the Drôme River but, counter to most  
305 patterns of stand development, decreased along the Rhône River. The mean diameter of *Populus* trees was  
306 much larger along the Rhône, and they achieved their maximum size much faster, within two decades (Figure  
307 5). This, combined with the decreasing density of these large, dominant trees later in the successional  
308 sequence had the effect of lowering *Populus* and overall stand basal area with time, in contrast to the Drôme,  
309 where both metrics increased.

310 Finally, sediment depth was a significant predictor for all stand basal area fractions (live, dead, and  
311 exotic trees), for *Fraxinus* density, and for *Acer spp.* basal area, mean diameter and density. However, the  
312 effect of sediment was positive for *Acer spp.* basal area and density but negative for *Fraxinus spp.* density and  
313 *Acer spp.* mean diameter (Table 3).

#### 314 **Differences in forest composition and structure between rivers**

315 The multivariate GLMs showed that forest structure was significantly influenced by forest stand age  
316 (Dev = 14.5,  $P = 0.031$ ), river (Dev = 73.8,  $P = 0.001$ ), sediment depth (Dev = 22.3,  $P = 0.034$ ) and the interaction  
317 term between age and river (Dev = 20.7,  $P = 0.043$ ). Based on the deviation explained by parameters, most of  
318 the variation in forest structure was related to differences between rivers; this dichotomy is well-represented  
319 by the separation of Rhône and Drôme plots along the first axis of the canonical analysis of principal  
320 coordinates (CAP 1, Figure 7A). The second axis was more evidently related to forest age, though some sites  
321 appeared to be well outside the predominant distribution. Univariate tests for each diameter class showed that  
322 the largest trees (DBH > 70 cm) had the highest test statistic values for the effect size between rivers (Dev =  
323 25.15,  $P_{\text{adj}} < 0.001$ ) (Appendix S9). Consequently, divergence in forest structure between the two rivers was  
324 mostly due to the greatest abundance of very large diameter trees within the Rhône River forests (mean basal  
325 area/plot = 8.17 m<sup>2</sup> ha<sup>-1</sup>) as compared to the Drôme River (mean basal area/plot = 0.11 m<sup>2</sup> ha<sup>-1</sup>).

326 As with forest structure, community composition was significantly influenced by river (Dev = 340.7,  $P =$   
327 0.001) and the interaction term between age and river (Dev = 49.6,  $P = 0.040$ ); this is similarly evident in the  
328 plot clustering along the first CAP axis (Figure 7B). However, community composition was much less influenced  
329 than forest structure by stand age (Dev = 40.2,  $P = 0.063$ ) and sediment depth (Dev = 33.2,  $P = 0.437$ ). The CAP  
330 plot shows that age classes were quite dispersed and randomly distributed along the second axis. Furthermore,  
331 the Drôme River plots were more clustered than the Rhône River plots, indicating greater similarity in tree  
332 species composition within the Drôme River corridor compared to the Rhône. Univariate tests for each tree  
333 species showed that *Acer negundo* has the largest effect size between the rivers (Dev = 130.30,  $P_{\text{adj}} < 0.001$ )  
334 (Appendix S10). Consequently, divergence in forest composition between the two rivers was in large part due  
335 to the absence of this exotic species within the Drôme River forests (mean plot basal area = 0.00 m<sup>2</sup> ha<sup>-1</sup>) as  
336 compared to the Rhône River (mean plot basal area = 5.37 m<sup>2</sup> ha<sup>-1</sup>).

337

#### 338 **Discussion**

339 Overall, the successional trajectories of riparian forests along the channelized and regulated bypassed  
340 channels of the Rhône River deviate from the expected historical trajectories, as represented by the  
341 unchannelized and unregulated reaches of the Drôme River . Though the riparian forests of the Drôme River  
342 are also under the influence of multiple human-induced stressors (Liébault and Piégay 2002), and though many  
343 trends in species composition and community functional traits followed expected forest stand trajectories,  
344 differences between the two rivers were stronger than the age gradient, which spanned 70 years in this study.  
345 Because the biogeographic setting and potential species pools are similar, these results strongly suggest that  
346 large differences in local environmental conditions are driving riparian forest development patterns (Clark et al.  
347 2019). Many of the shifts along the Rhône River chronosequence were more pronounced and rapid compared  
348 to the Drôme, in particular for foundation species (e.g., *Populus* spp.) and invasive exotic species (e.g., *Acer*  
349 *negundo*) (Figure 8). In light of these rapid and profound divergences in community composition and structure,  
350 mostly related to cumulative effect of human-induced stressors, it may be argued that the resulting riparian  
351 forests correspond to the definition of a “novel ecosystem” (Hobbs et al. 2009). Indeed, the riparian forests of  
352 Rhône River are rapidly dominated by non-native species, and the greatly suppressed disturbance regime  
353 (Vázquez-Tarrió et al. 2019) and lack of pioneer forest regeneration along bypassed channels, impedes  
354 community dynamics processes evident in more natural reference systems ( e.g., Stella et al. in review, Fierke  
355 and Kauffman 2005, Balian and Naiman 2005). In this severely degraded system, it therefore seems more  
356 pragmatic to prioritize management and restoration measures toward desired human benefits rather than  
357 target a return to a potential reference state (Dufour and Piégay 2009).

### 358 **Flow regulation and channelization induce rapid changes in abiotic conditions**

359 Strongly divergent trends in abiotic conditions were evident between the two river systems. While it  
360 cannot be ruled out that natural differences in physical and ecological conditions between the Drôme and the  
361 Rhône watersheds could be a driver behind this observed effect, we inferred that the different management  
362 histories of the Rhône and Drôme is one of the most important ecological drivers. Along the highly artificial,  
363 stable river margins of the Rhône River, the Girardon dike structures were very effective in trapping suspended  
364 sediment, with very high accumulation rates of overbank fine sediment, especially immediately after the initial  
365 channelization and prior to the dam construction period (for further details see, Tena et al. 2020). Large  
366 quantities of fine sediment trapped along channelized river margins have been shown to increase ecosystem  
367 productivity by maintaining higher nutrient pools (Franklin et al. 2009). In addition, high overbank

368 sedimentation rates induce strong differences in soil properties (e.g., texture and moisture retention), which  
369 can also promote a resource-rich environment. These factors may explain the rapid and vigorous growth of  
370 pioneer trees, particularly *Populus* species that reached maximum tree sizes very quickly, i.e., at a very early  
371 stage in the succession sequence. Overall, the increase in bank accretion, the decrease in overbank flows  
372 (Figure 2) as well as the lowering of the water table due to river entrenchment, has induced gradual  
373 disconnection between the channelized margins and the main channel. This has ultimately led to changes in  
374 channel morphology and physical conditions on the Rhône, i.e., a shift from anabranching reaches to narrow,  
375 very stable, single thread channels (Tena et al. 2020), as has been shown on other rivers (Wilcock and Essery  
376 1991, Marston et al. 1995).

377           Disconnection of the riparian zone from the river channel is even more exacerbated by changes in the  
378 hydrologic regime, as evidenced by the decrease in the mean annual flow along the Rhône River since the  
379 1940s. This decrease is mainly due to water diversion into lateral canals following the construction of multiple  
380 hydropower dams in the post-war period, which were commissioned at different dates along the Rhône  
381 corridor (i.e., DZM = 1952, MON = 1957, PBN = 1966, PDR = 1977, see also Figure 2). The combined effects of  
382 high overbank sedimentation rates and pronounced decreases in the mean annual discharge induced a loss of  
383 up to 60% of the active channel surface of the Rhône River (Tena et al. 2020). Tena et al. (2020) found that  
384 along the bypassed channels the terrestrialization process and associated vegetation encroachment were  
385 primarily driven by the Girardon dike structures (i.e., channelization) rather than by flow regulation. The  
386 cumulative effects of channel correction and regulation can also induce a rapid decline in the groundwater  
387 table and thus a more limited access to soil water for existing riparian trees (Franklin et al. 2009), which on the  
388 Rhône River may have been amplified locally by gravel extraction and pumping for irrigation (Thorel et al.  
389 2018). Finally, channelization and flow regulation may reduce the variability of hydrologic conditions, especially  
390 lower intensity and frequency of flooding on higher riparian floodplains, as well as bedload transport capacities  
391 (Vázquez-Tarrío et al. 2019). Conversely, along the Drôme River, low rate of fine sediment accumulation and  
392 maintenance of a natural flow regime likely promote a dynamic equilibrium across successional phases without  
393 the rapid change in floodplain conditions that both correction and regulation induced on the Rhône (Figure 8).  
394 Overall, our results pointed out profound changes in hydro-geomorphic processes between the two river  
395 systems. In this view, we suggest that the artificially stabilizing effect of the combined Girardon structures and

396 flow regulation on the Rhône River enabled the development of a distinct and potentially unique riparian forest  
397 community (Thorel et al. 2018).

398 **Changes in abiotic conditions strongly alter the functional, structural and compositional attributes of riparian**  
399 **forests**

400 Consistent with changes in abiotic conditions over time, our results demonstrate rapid divergence in  
401 riparian forest dynamics between the two river systems, reflecting environmental selection toward a pool of  
402 traits and species best adapted to local conditions (Figure 8). Although successional shifts in plant functional  
403 traits followed predictable successional trajectories along both rivers, (e.g., Fierke and Kauffman 2005, Van Pelt  
404 et al. 2006, Muñoz-Mas et al. 2017), increases in wood density and SLA values within the riparian forest were  
405 faster along the Rhône River (Figure 3). Specifically, our results show that channelization and flow regulation  
406 accelerate the transition from a disturbance-dependent pioneer community, i.e., fast-growing tree species with  
407 high resource acquisition strategies, to a post-pioneer community dominated by slow-growing, competitive  
408 species with high resource conservation and retention strategies (Marston et al. 1995, Oswalt and King 2005).  
409 This accelerated shift in plant ecological strategy is likely related to both a more limited access to groundwater  
410 and high overbank sedimentation rates promoting resource-rich environments along the Rhône, both of which  
411 were mediated by changes to the hydrologic and disturbance regimes (Figure 2) (see also, Vázquez-Tarrío et al.  
412 2019). Consequently, there has been a major divergence in plant habitat niches between the two river systems,  
413 and large corresponding differences in stand attributes (Figure 4), plant assemblages (Figure 7) and forest  
414 successional pathways. These results reinforce the importance of contingent factors in determining ecological  
415 trajectories, as has been shown for old fields and other successional contexts (e.g., Clark et al. 2019)

416 Prolonged and rapid decline in the groundwater table has been shown to greatly alter growth and  
417 survival of pioneer species requiring permanent access to soil water (Reily and Johnson 1982, Scott et al. 1999,  
418 Lite and Stromberg 2005, Stella et al. 2013a), and favor more competitive species such as post-pioneer and  
419 exotic species (Merritt and Poff 2010, González et al. 2010, Nadal-Sala et al. 2017). Within the region  
420 encompassed by our study, radial growth of *Populus nigra*, an obligate phreatophyte that dominates early  
421 successional forest stands, is more sensitive to groundwater manipulation compared to the mesophytic species  
422 *Fraxinus excelsior*, which can use both soil moisture and deeper groundwater opportunistically to maintain  
423 more constant inter-annual growth (Singer et al. 2013). Relative basal area and mean diameter of post-pioneer  
424 species, including *Fraxinus* spp. and *Acer* spp., increased over time in both rivers. For *Populus* species, however,



425 while tree diameter and stem density varied consistently between the two rivers, the basal area increased  
426 along the Drôme but decreased along the Rhône. In addition, most of the divergence in species composition  
427 between the two river systems was due to the great abundance of the exotic invasive species *Acer negundo*  
428 along the Rhône River. Compared to native pioneer and post-pioneer tree species, *Acer negundo* shows higher  
429 level of plasticity in foliage allocation (i.e., larger specific leaf area and total leaf area) when resources are not  
430 limiting, thus allowing for better growth and survival (Porté et al. 2011). Thus, the temporal trends in whole-  
431 stand (Figure 4) and genus-specific (Figure 5) tree distributions suggest that channelization and flow regulation  
432 have promoted a resource-rich environment within the Girardon structures (Tena et al. 2020), leading to an  
433 acceleration of ecological succession due to faster growth and mortality of native pioneer species and to better  
434 survival and establishment of stress tolerant species, including exotic species (Catford et al. 2014).

435 Resource-rich environments also benefit native species, in particular high growth rates of *Salicaceae*  
436 species (Karrenberg et al. 2002) and other, more competitive species (e.g., Porté et al. 2011, Nadal-Sala et al.  
437 2017). The Rhône River experienced much faster biomass accumulation, mostly due to the greater abundance  
438 of very large trees that achieved their maximum size within 20 years. Contrary to expectations, however, basal  
439 area and mean tree diameter of both live and dead fractions decreased with stand age along the Rhône River.  
440 The anomalous pattern on the Rhône was mostly due to the scarcity of very large pioneer trees (primarily *Salix*  
441 spp. and *Populus* spp.) in mature forest stands. Though they are generally short-lived trees, their rapid  
442 reduction in density along the Rhône meant that overall basal area decreased on that river with forest age,  
443 whereas it continued to increase on the Drôme, as expected. Since biomass usually increases along the initial  
444 successional phases in riparian forests (e.g., Fierke and Kauffman 2005, Balian and Naiman 2005, Van Pelt et al.  
445 2006), even along regulated rivers (Stella et al. in review), these results suggest that several interacting  
446 stressors may be responsible for the unusual patterns. One explanation may be the rapid dewatering and  
447 hydric stress that followed flow reductions in the bypassed channels with the operation of the post-war  
448 hydropower canals. This would have preferentially affected older, established trees that could not adjust to the  
449 new groundwater regime, increasing mortality of pioneer trees and reducing the growth rate of survivors in the  
450 oldest stands. Another potential factor is selective cutting of larger trees along levees and dikes, which was  
451 sometimes conducted by farmers and/or river managers of the “Compagnie Nationale du Rhône” in order to  
452 protect the structural integrity of dikes and limit large wood inputs to the main channel. As such, patterns  
453 observed along the Rhône River most likely result from cumulative multiple stressors related to human activity,

454 mainly channelization and flow regulation but also occasionally selective cutting, which are difficult to  
455 disentangle from other drivers (Stella and Bendix 2018).

456         The increase in trait dispersion over time (Figure 3) indicates that older floodplain forests increasingly  
457 support co-occurring species with contrasting ecological strategies (Figure 3). Hydro-geomorphic changes over  
458 time not only drive changes in abiotic conditions at the floodplain scale but may also induce greater habitat  
459 heterogeneity at finer scale, potentially due to greater variability in topographic and hydrologic conditions.  
460 Accordingly, several authors have reported an increase in tree species richness with later successional stages in  
461 riparian forests (Schnitzler 1995, Nakamura et al. 1997, Van Pelt et al. 2006). Here, we showed that ecological  
462 succession in riparian forests not only promotes taxonomic diversity (Figure 6) but also functional diversity  
463 (Figure 3). The contrasts in functional traits between rivers suggest that the riparian forests of the Rhône River  
464 underwent a more rapid change to functionally different species assemblages compared to the Drôme. Indeed,  
465 our results show that the shift in community-weighted SLA and wood density was accelerated along the Rhône  
466 River (Figure 3). In contrast, the trait dispersion for seed mass was more pronounced along the Drôme River,  
467 indicating a higher occurrence of tree species with small seed mass (i.e., mostly *Salicaceae*) in older stands.  
468 Given the importance of floods and hydrochory in maintaining early successional forest stands (Scott et al.  
469 1997, Fraaije et al. 2017), the greater representation of pioneer species within more successional stages on the  
470 Drôme River further confirms the influence of dynamic fluvial processes (e.g., flooding, channel migration) in  
471 riparian successional processes on intact rivers, compared to a stabilized and controlled environment as on the  
472 Rhône .

473

#### 474 **Conclusion**

475         In comparing successional trajectories between the heavily modified Rhône and more natural Drôme  
476 rivers, we found that the legacy of cumulative impacts of river channelization and flow regulation strongly  
477 altered the structure, composition and ecological trajectory of riparian forests. These findings accord with prior  
478 studies along heavily modified rivers (Merritt and Cooper 2000, Nakamura et al. 2002, Oswalt and King 2005,  
479 Dufour et al. 2007, González et al. 2010, Johnson et al. 2012). By using a chronosequence modelling approach,  
480 we illustrated the parallel changes in river conditions, riparian forest structure and composition, and functional  
481 trait expression within the plant community along a successional gradient. Thus, although the earliest phase of  
482 stand development (< 20 years) on both rivers was characterized by the dominance of pioneer and

483 disturbance-dependent species, the shift to a mature forest stage dominated by post-pioneer and exotic  
484 species was greatly accelerated (within 20-50 years) along the Rhône River (Figure 8). Beyond differences not  
485 related to human-induced stressors, this accelerated shift was likely linked to the fact that the Rhône River  
486 margins have experienced a more rapid terrestrialization than natural floodplains, due to the combined effect  
487 of less frequent and lower magnitude flooding events, greater overbank fine sediment deposition, and a  
488 decline in groundwater tables due to flow diversion. Thus, by disrupting natural hydro-geomorphological  
489 processes at different spatial and temporal scales, channelization and flow regulation have induced severe and  
490 long-term changes in environmental conditions, in turn driving riparian plant communities far from their  
491 historical reference trajectories (Figure 7). Due to the strong differences in the biotic community, as well as  
492 their abiotic drivers, we suggest that restoration of the Rhône River riparian forests to a more natural (i.e., pre-  
493 development) state is highly improbable, even if physical conditions such as flooding and bank revetment are  
494 mitigated by restoration actions. The novel structural, compositional and functional attributes of the Rhône  
495 riparian forest, including the dominance of non-native species in the regeneration fraction and understory,  
496 suggest that the forest will be highly resistant to change and that process-based restoration actions would  
497 likely have a long and persistent hysteresis (Suding et al. 2004). In this system as in other severely degraded  
498 ones, riparian management may benefit from a more pragmatic approach focusing on desired human benefits  
499 (Dufour and Piégay 2009) and specific ecological targets (Palmer et al. 2005). For the Rhône River's riparian  
500 forest, which is increasingly valued for its ecological and cultural legacy, these approaches may include active  
501 stand management by selective cutting to remove exotic species and enhance native tree diversity, promoting  
502 through active and passive means and pioneer stages which are no longer rejuvenated, as well as enhancing  
503 other ecosystem services such as flood and pollutant mitigation, carbon storage, and habitat quality for wildlife  
504 and fish.

505

#### 506 **Authors' contributions**

507 P.J., J.C.S., H.P. and A.E. conceived and designed the experiments. J.C.S., B.R., P.B., J-M.F. and C.J. collected the  
508 data. P.J. analysed the data and wrote the first draft of the manuscript. All authors contributed critically to the  
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510

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519

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732

733 Table 1. Variation in independent and dependent variables between the rivers Drôme (n = 69 plots) and Rhône  
 734 (n = 65 plots), France (CWM = community-weighted mean, FDis = functional dispersion, SLA = specific leaf  
 735 area).

Measure	Variable	Drôme River		Rhône River	
		mean ( $\pm$ SD)	range	mean ( $\pm$ SD)	range
Plot description					
	Forest stand age (years)	31.3 ( $\pm$ 20.3)	5.0 - 62.0	44.6 ( $\pm$ 18.6)	16.0 - 76.0
	Sediment depth (cm)	42 ( $\pm$ 36)	0 - 140	249 ( $\pm$ 121)	24 - 490
	Mean annual flow (m <sup>3</sup> )	18.4 ( $\pm$ 4.6)	7.3 - 31.3	527.2 ( $\pm$ 402.4)	77.7 - 1550.4
Functional traits					
CWM	SLA	12.63 ( $\pm$ 1.66)	10.0 - 17.0	14.87 ( $\pm$ 3.00)	11.1 - 21.8
	Wood density	0.41 ( $\pm$ 0.05)	0.3 - 0.6	0.47 ( $\pm$ 0.10)	0.3 - 0.7
	Seed mass	1.40 ( $\pm$ 0.90)	0.4 - 4.2	1.63 ( $\pm$ 1.04)	0.2 - 3.8
FDis	SLA	0.24 ( $\pm$ 0.20)	0.0 - 0.7	0.40 ( $\pm$ 0.26)	0.0 - 1.0
	Wood density	0.51 ( $\pm$ 0.39)	0.0 - 1.2	0.69 ( $\pm$ 0.44)	0.0 - 1.4
	Seed mass	0.41 ( $\pm$ 0.36)	0.0 - 1.4	0.40 ( $\pm$ 0.25)	0.0 - 1.1
Stand attributes					
Basal area (m <sup>2</sup> ha <sup>-1</sup> )	Live trees	15.47 ( $\pm$ 9.76)	0.1 - 38.7	27.65 ( $\pm$ 10.85)	6.3 - 57.8
	Dead trees	3.72 ( $\pm$ 3.69)	0.0 - 18.0	5.13 ( $\pm$ 4.43)	0.0 - 22.3
	Exotic trees	0.58 ( $\pm$ 1.10)	0.0 - 5.2	8.22 ( $\pm$ 9.92)	0.0 - 42.8
Mean diameter (cm)	Live trees	17.49 ( $\pm$ 4.91)	8.7 - 30.7	24.91 ( $\pm$ 8.02)	10.7 - 47.7
	Dead trees	15.60 ( $\pm$ 5.63)	9.0 - 44.2	28.96 ( $\pm$ 16.97)	9.9 - 76.6
	Exotic trees	13.7 ( $\pm$ 4.23)	8.0 - 24.4	17.49 ( $\pm$ 6.11)	7.5 - 35.4
Stem density (n ha <sup>-1</sup> )	Live trees	504 ( $\pm$ 262.65)	16 - 1066	463 ( $\pm$ 241.09)	71 - 1169
	Dead trees	157 ( $\pm$ 107.85)	0 - 500	98 ( $\pm$ 99.12)	0 - 453
	Exotic trees	38 ( $\pm$ 80.39)	0 - 466	276 ( $\pm$ 225.97)	0 - 1122
Tree genera					
Basal area (m <sup>2</sup> ha <sup>-1</sup> )	<i>Populus</i> spp.	11.44 ( $\pm$ 8.87)	0.00 - 38.59	14.83 ( $\pm$ 11.90)	0.00 - 43.97
	<i>Fraxinus</i> spp.	1.03 ( $\pm$ 1.76)	0.00 - 7.28	1.59 ( $\pm$ 2.71)	0.00 - 14.08
	<i>Acer</i> spp.	1.43 ( $\pm$ 2.54)	0.00 - 11.74	4.04 ( $\pm$ 4.52)	0.00 - 19.10
Mean diameter (cm)	<i>Populus</i> spp.	21.22 ( $\pm$ 7.27)	8.01 - 43.60	54.15 ( $\pm$ 16.20)	26.78 - 113.00
	<i>Fraxinus</i> spp.	13.64 ( $\pm$ 3.99)	8.00 - 23.33	23.54 ( $\pm$ 12.82)	8.50 - 68.50
	<i>Acer</i> spp.	14.58 ( $\pm$ 3.65)	8.00 - 22.00	20.62 ( $\pm$ 10.34)	7.50 - 60.50
Stem density (n ha <sup>-1</sup> )	<i>Populus</i> spp.	268 ( $\pm$ 180.38)	0 - 833	97 ( $\pm$ 129.87)	0 - 604
	<i>Fraxinus</i> spp.	53 ( $\pm$ 93.35)	0 - 600	58 ( $\pm$ 113.75)	0 - 652
	<i>Acer</i> spp.	72 ( $\pm$ 128.49)	0 - 633	157 ( $\pm$ 162.13)	0 - 636
Diversity indices					
	Diameter classes	1.59 ( $\pm$ 0.43)	0.0 - 2.1	1.94 ( $\pm$ 0.29)	0.8 - 2.4
	Tree species	0.79 ( $\pm$ 0.56)	0.0 - 1.7	0.96 ( $\pm$ 0.37)	0.0 - 1.7

736

737 Table 2. Top-ranking models predicting variations in abiotic drivers and biotic responses over time along the  
738 rivers Drôme and Rhône, France, as assessed with Akaike's information criterion corrected for small sample  
739 size (AIC<sub>c</sub>). Other model information provided include the number of estimated parameters including the  
740 intercept (k), AIC<sub>c</sub> weight (W) and adjusted coefficient of determination (R<sup>2</sup>). Asterisks in the model formulas  
741 indicate an interaction term (CWM = community-weighted mean, FDis = functional dispersion, SLA = specific  
742 leaf area).

Measure	Dependent variable	Top-ranked model	k	W	R <sup>2</sup>
Abiotic drivers					
	Sediment depth	Age * River	5	0.823	0.564
	Mean annual flow	Year * River	5	0.941	0.476
	SD annual flow	Year	5	0.425	0.108
Functional traits					
CWM	SLA	Age * River	5	0.423	0.387
	Wood density	Age * River	5	0.399	0.430
	Seed mass	Age	3	0.282	0.376
FDis	SLA	Age + River	4	0.373	0.232
	Wood density	Age * River	5	0.305	0.228
	Seed mass	Age * River	5	0.500	0.300
Stand attributes					
Basal area	Live trees	Age * River + Sed_depth	6	0.775	0.290
	Dead trees	Age * River + Sed_depth	6	0.978	0.174
	Exotic trees	Age * River + Sed_depth	6	0.962	0.578
Mean diameter	Live trees	Age * River	5	0.632	0.332
	Dead trees	Age* River + Sed_depth	6	0.857	0.155
	Exotic trees	Age* River	5	0.378	0.183
Stem density	Live trees	Age + River + Sed_depth	5	0.612	0.139
	Dead trees	Age * River + Sed_depth	6	0.297	0.117
	Exotic trees	Age + River	4	0.417	0.490
Tree genera					
Basal area	<i>Populus</i> spp.	Age * River	5	0.720	0.079
	<i>Fraxinus</i> spp.	Age + Sed_depth	4	0.351	0.228
	<i>Acer</i> spp.	Age * River + Sed_depth	6	0.584	0.344
Mean diameter	<i>Populus</i> spp.	Age* River	5	0.482	0.706
	<i>Fraxinus</i> spp.	Age + River	4	0.407	0.295
	<i>Acer</i> spp.	Age + River + Sed_depth	5	0.574	0.182
Stem density	<i>Populus</i> spp.	Age * River	5	0.617	0.328
	<i>Fraxinus</i> spp.	Age + Sed_depth	4	0.457	0.180
	<i>Acer</i> spp.	Age * River + Sed_depth	6	0.944	0.397
Diversity indices					
	Diameter classes	Age * River	5	0.435	0.241
	Tree species	Age * River	5	0.731	0.247

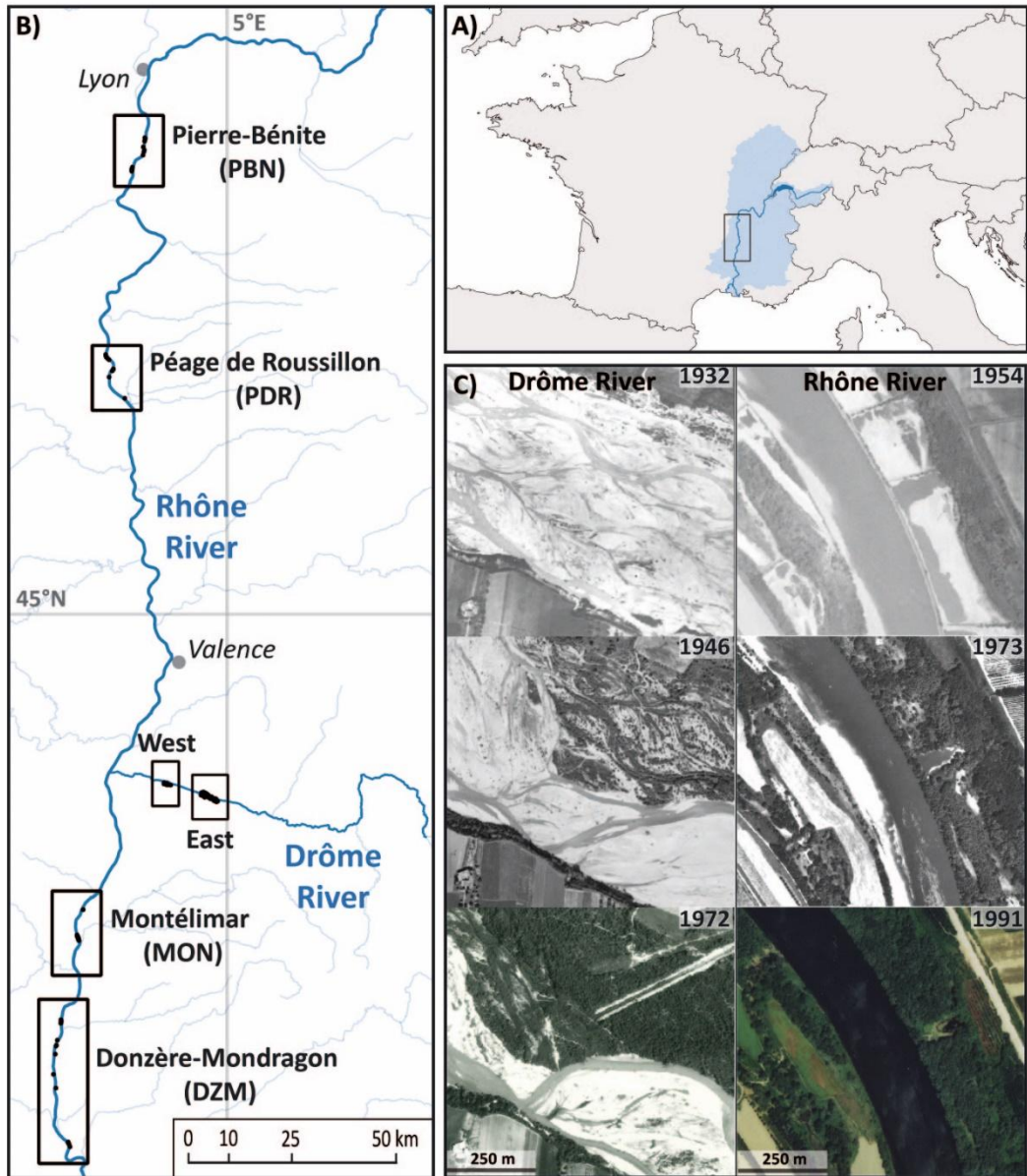
743

744 Table 3. Standardized coefficient estimates ( $\pm$ SE) and confidence intervals (95% CI) for each variable used to predict mean and dispersion of functional trait values, basal  
745 area, mean diameter and stem density of stand attributes and of tree genera as well as diversity indices to forest stand age along the rivers Drôme and Rhône, France. Bold  
746 font indicates coefficient estimates for which the 95% confidence interval excludes zero (CWM = community-weighted mean, FDis = functional dispersion, SLA = specific leaf  
747 area).

Measure	Variable	Age		River		Age*River		Sed_depth	
		Estimate ( $\pm$ SE)	(95% CI)	Estimate ( $\pm$ SE)	(95% CI)	Estimate ( $\pm$ SE)	(95% CI)	Estimate ( $\pm$ SE)	(95% CI)
Functional traits									
CWM:	SLA	<b>0.052 (<math>\pm</math>0.017)</b>	<b>(0.019; 0.085)</b>	<b>0.095 (<math>\pm</math>0.026)</b>	<b>(0.044; 0.146)</b>	<b>0.069 (<math>\pm</math>0.026)</b>	<b>(0.018; 0.120)</b>	NA	NA
	Wood density	<b>0.075 (<math>\pm</math>0.017)</b>	<b>(0.042; 0.108)</b>	<b>0.065 (<math>\pm</math>0.025)</b>	<b>(0.016; 0.114)</b>	<b>0.060 (<math>\pm</math>0.025)</b>	<b>(0.011; 0.109)</b>	NA	NA
	Seed mass	<b>0.603 (<math>\pm</math>0.067)</b>	<b>(0.472; 0.734)</b>	NA	NA	NA	NA	NA	NA
FDis:	SLA	<b>0.073 (<math>\pm</math>0.014)</b>	<b>(0.046; 0.100)</b>	<b>0.062 (<math>\pm</math>0.029)</b>	<b>(0.005; 0.119)</b>	NA	NA	NA	NA
	Wood density	<b>0.162 (<math>\pm</math>0.029)</b>	<b>(0.105; 0.219)</b>	0.039 ( $\pm$ 0.044)	(-0.047; 0.125)	<b>-0.092 (<math>\pm</math>0.044)</b>	<b>(-0.178; -0.006)</b>	NA	NA
	Seed mass	<b>0.167 (<math>\pm</math>0.022)</b>	<b>(0.124; 0.210)</b>	-0.065 ( $\pm$ 0.034)	(-0.132; 0.002)	<b>-0.113 (<math>\pm</math>0.034)</b>	<b>(-0.180; -0.046)</b>	NA	NA
Stand attributes									
Basal area:	Live trees	<b>0.365 (<math>\pm</math>0.100)</b>	<b>(0.169; 0.561)</b>	0.413 ( $\pm$ 0.218)	(-0.014; 0.840)	<b>-0.567 (<math>\pm</math>0.153)</b>	<b>(-0.867; -0.267)</b>	<b>0.256 (<math>\pm</math>0.119)</b>	<b>(0.023; 0.489)</b>
	Dead trees	<b>0.270 (<math>\pm</math>0.087)</b>	<b>(0.099; 0.441)</b>	-0.343 ( $\pm$ 0.188)	(-0.711; 0.025)	<b>-0.452 (<math>\pm</math>0.132)</b>	<b>(-0.711; -0.193)</b>	<b>0.379 (<math>\pm</math>0.103)</b>	<b>(0.177; 0.581)</b>
	Exotic trees	-0.003 ( $\pm$ 0.086)	(-0.172; 0.166)	<b>0.798 (<math>\pm</math>0.186)</b>	<b>(0.433; 1.163)</b>	<b>0.461 (<math>\pm</math>0.130)</b>	<b>(0.206; 0.716)</b>	<b>0.304 (<math>\pm</math>0.101)</b>	<b>(0.106; 0.502)</b>
Mean tree diameter:	Live trees	0.064 ( $\pm$ 0.034)	(-0.003; 0.131)	<b>0.373 (<math>\pm</math>0.051)</b>	<b>(0.273; 0.473)</b>	<b>-0.209 (<math>\pm</math>0.051)</b>	<b>(-0.309; -0.109)</b>	NA	NA
	Dead trees	0.077 ( $\pm$ 0.051)	(-0.023; 0.177)	<b>0.374 (<math>\pm</math>0.107)</b>	<b>(0.164; 0.584)</b>	<b>-0.356 (<math>\pm</math>0.077)</b>	<b>(-0.507; -0.205)</b>	<b>0.141 (<math>\pm</math>0.058)</b>	<b>(0.027; 0.255)</b>
	Exotic trees	0.033 ( $\pm$ 0.053)	(-0.071; 0.137)	<b>0.159 (<math>\pm</math>0.069)</b>	<b>(0.024; 0.294)</b>	0.123 ( $\pm$ 0.070)	(-0.014; 0.260)	NA	NA
Stem density:	Live trees	<b>0.147 (<math>\pm</math>0.061)</b>	<b>(0.027; 0.267)</b>	<b>-0.560 (<math>\pm</math>0.165)</b>	<b>(-0.883; -0.237)</b>	NA	NA	<b>0.280 (<math>\pm</math>0.089)</b>	<b>(0.106; 0.454)</b>
	Dead trees	<b>0.513 (<math>\pm</math>0.181)</b>	<b>(0.158; 0.868)</b>	<b>-1.449 (<math>\pm</math>0.394)</b>	<b>(-2.221; -0.677)</b>	-0.409 ( $\pm$ 0.276)	(-0.950; 0.132)	0.391 ( $\pm$ 0.215)	(-0.030; 0.812)
	Exotic trees	-0.024 ( $\pm$ 0.154)	(-0.326; 0.278)	<b>3.327 (<math>\pm</math>0.307)</b>	<b>(2.725; 3.929)</b>	NA	NA	NA	NA
Tree genera									
Basal area:	<i>Populus</i> spp.	0.143 ( $\pm$ 0.115)	(-0.082; 0.368)	0.248 ( $\pm$ 0.172)	(-0.089; 0.585)	<b>-0.594 (<math>\pm</math>0.173)</b>	<b>(-0.933; -0.255)</b>	NA	NA
	<i>Fraxinus</i> spp.	<b>0.372 (<math>\pm</math>0.060)</b>	<b>(0.254; 0.490)</b>	NA	NA	NA	NA	-0.095 ( $\pm$ 0.060)	(-0.213; 0.023)
	<i>Acer</i> spp.	<b>0.476 (<math>\pm</math>0.089)</b>	<b>(0.302; 0.650)</b>	0.181 ( $\pm$ 0.192)	(-0.195; 0.557)	<b>-0.347 (<math>\pm</math>0.135)</b>	<b>(-0.612; -0.082)</b>	<b>0.212 (<math>\pm</math>0.105)</b>	<b>(0.006; 0.418)</b>
Mean tree	<i>Populus</i> spp.	<b>0.142 (<math>\pm</math>0.039)</b>	<b>(0.066; 0.218)</b>	<b>0.909 (<math>\pm</math>0.058)</b>	<b>(0.795; 1.023)</b>	<b>-0.124 (<math>\pm</math>0.059)</b>	<b>(-0.240; -0.008)</b>	NA	NA

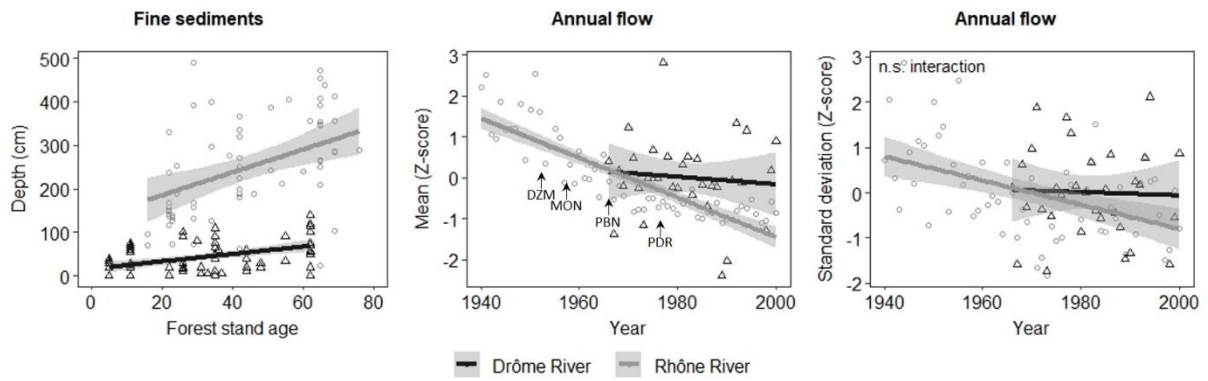
diameter:	<i>Fraxinus</i> spp.	<b>0.131 (±0.048)</b>	<b>(0.037; 0.225)</b>	<b>0.392 (±0.092)</b>	<b>(0.212; 0.572)</b>	NA	NA	NA	NA
	<i>Acer</i> spp.	<b>0.177 (±0.051)</b>	<b>(0.077; 0.277)</b>	<b>0.448 (±0.127)</b>	<b>(0.199; 0.697)</b>	NA	NA	<b>-0.135 (±0.063)</b>	<b>(-0.258; -0.012)</b>
Stem	<i>Populus</i> spp.	-0.004 (±0.151)	(-0.300; 0.292)	<b>-1.380 (±0.226)</b>	<b>(-1.823; -0.937)</b>	<b>-0.606 (±0.228)</b>	<b>(-1.053; -0.159)</b>	NA	NA
density:	<i>Fraxinus</i> spp.	<b>1.062 (±0.191)</b>	<b>(0.688; 1.436)</b>	NA	NA	NA	NA	<b>-0.605 (±0.191)</b>	<b>(-0.979; -0.231)</b>
	<i>Acer</i> spp.	<b>1.506 (±0.228)</b>	<b>(1.059; 1.953)</b>	0.159 (±0.496)	(-0.813; 1.131)	<b>-1.483 (±0.347)</b>	<b>(-2.163; -0.803)</b>	<b>0.755 (±0.270)</b>	<b>(0.226; 1.284)</b>
Diversity indexes									
	Diameter classes	<b>0.159 (±0.043)</b>	<b>(0.075; 0.243)</b>	<b>0.284 (±0.065)</b>	<b>(0.157; 0.411)</b>	<b>-0.133 (±0.065)</b>	<b>(-0.260; -0.006)</b>	NA	NA
	Tree species	<b>0.330 (±0.052)</b>	<b>(0.228; 0.432)</b>	0.048 (±0.077)	(-0.103; 0.199)	<b>-0.277 (±0.078)</b>	<b>(-0.430; -0.124)</b>	NA	NA

748 Figure 1. Map of the study area within the Rhône River basin (A); location of the study reaches along the Drôme  
 749 and Rhône rivers (B); and examples of aerial photograph series showing the riparian forest development along  
 750 the two rivers (C, aerial photographs: IGN).

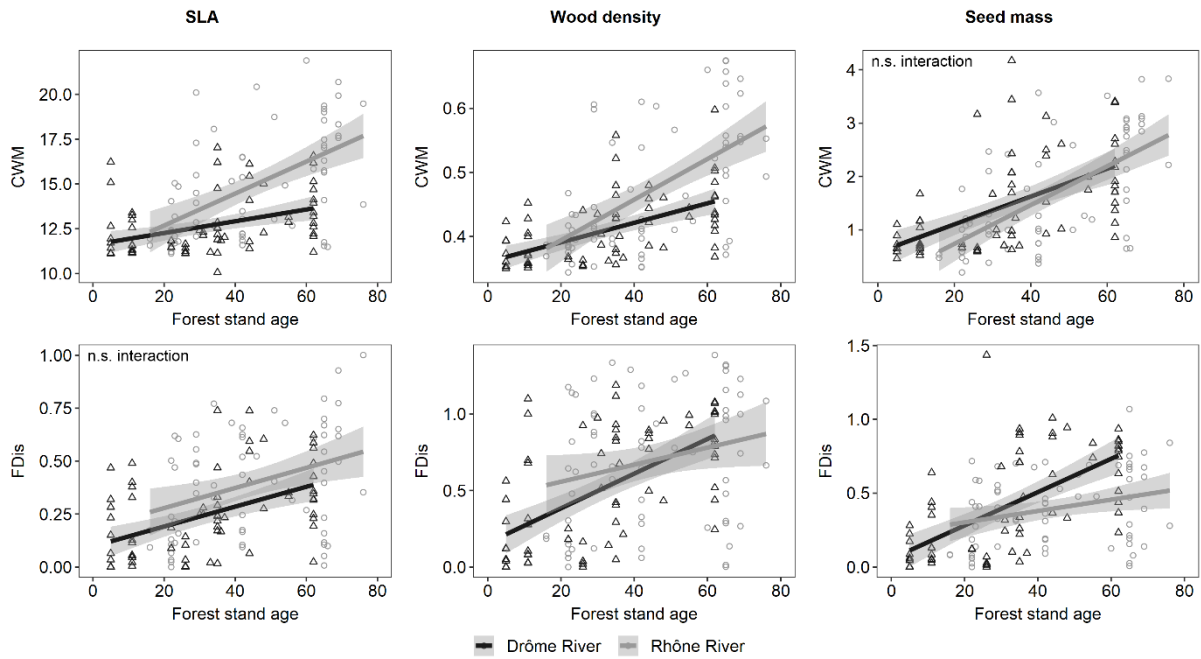




751 Figure 2. Variation in fine sediment depth with forest stand age along the rivers Drôme and Rhône and trends  
 752 in the mean and standard deviation (SD) of annual flow since 1940. Annual flow variables were standardized to  
 753 account for differences in basin size between rivers (n.s. interaction = non-significant Year x River interaction;  
 754 see Appendix S8). To facilitate interpretation, the dates of commissioning of the diversion canals are shown  
 755 with arrows in the figure (i.e., DZM = 1952, MON = 1957, PBN = 1966, PDR = 1977).

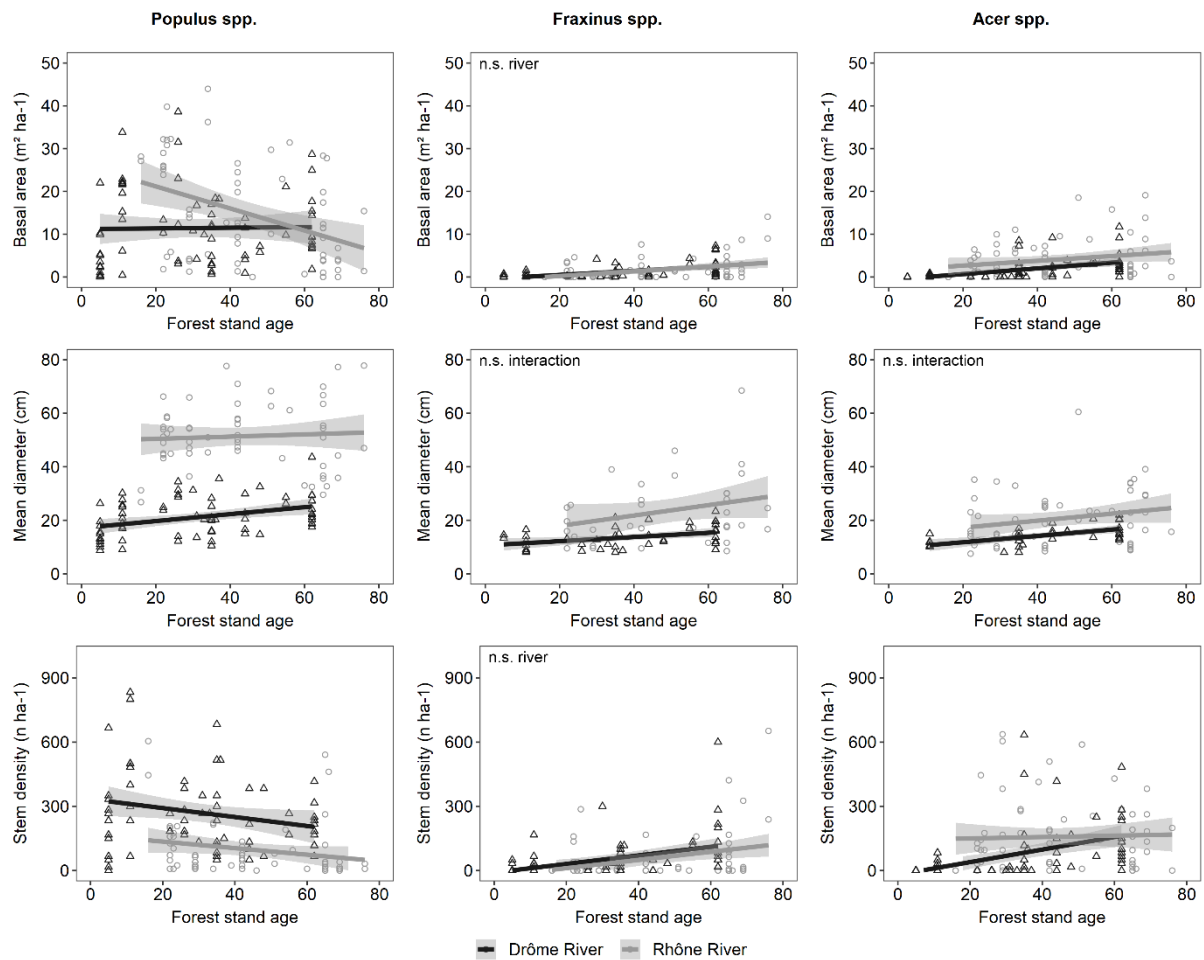


756 Figure 3. Variation in the mean (CWM) and dispersion (FDIs) of specific leaf area (SLA,  $\text{m}^2 \text{kg}^{-1}$ ), wood density  
 757 ( $\text{g cm}^3$ ) and seed mass (mg) with forest stand age along the rivers Drôme and Rhône (n.s. interaction = non-  
 758 significant Age x River interaction; see Table 3). Trait values and their variation increased more rapidly along  
 759 the Rhône River for SLA and wood density, compared to the Drôme.



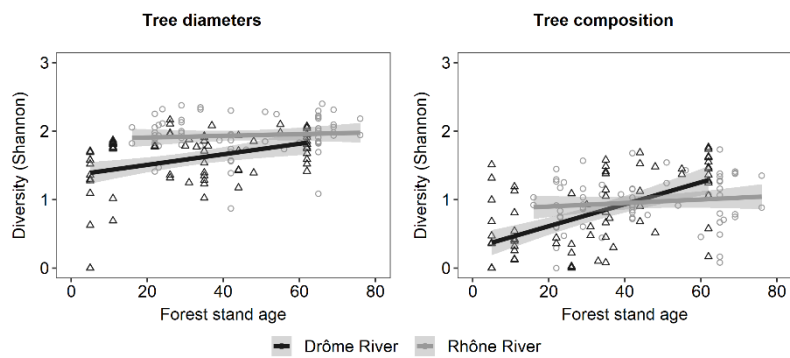


764 Figure 5. Variation in the basal area, mean diameter and stem density of *Populus* spp., *Fraxinus* spp. and *Acer*  
 765 spp. with forest stand age along the rivers Drôme and Rhône (n.s river = non-significant River effect; see Table  
 766 3). Whereas development of *Fraxinus* spp., a native post-pioneer taxon, was comparable among rivers, the  
 767 overall divergence in successional trajectories (Figure 4) was driven by greater *Populus* spp. tree size and basal  
 768 area, as well as the higher density and basal area of non-native *Acer* species, primarily *Acer negundo*, within the



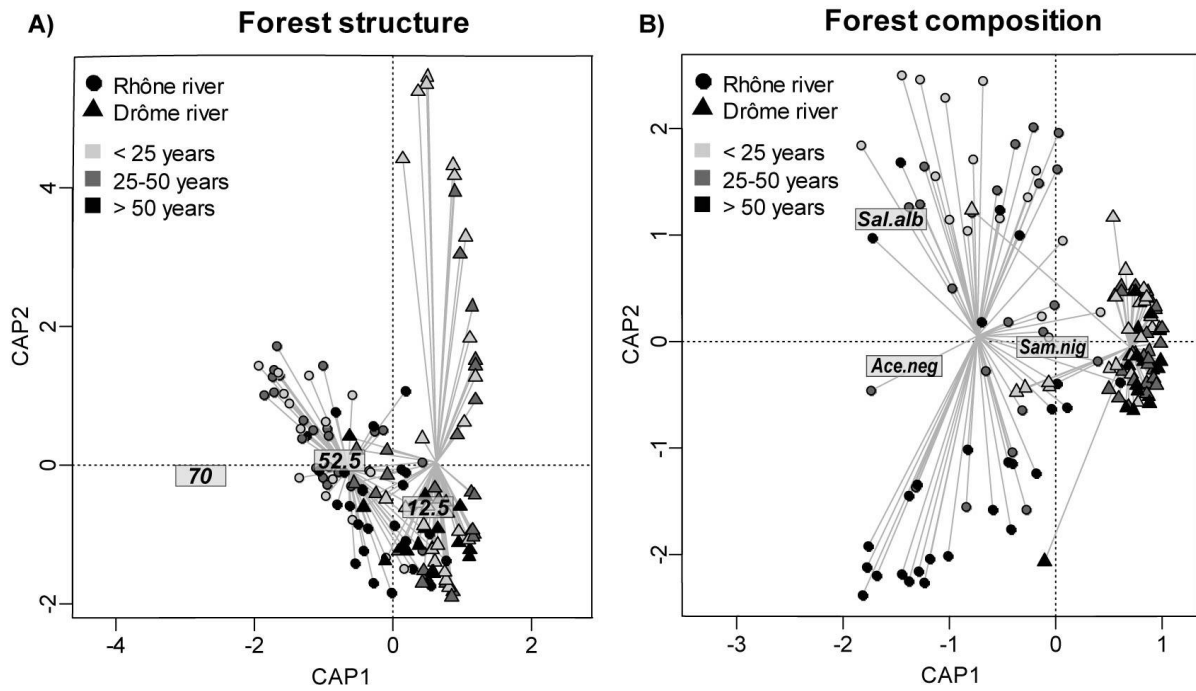
769 Rhône River riparian forest community.

770 Figure 6. Variation in the diversity of tree diameter classes and tree species with forest stand age along the

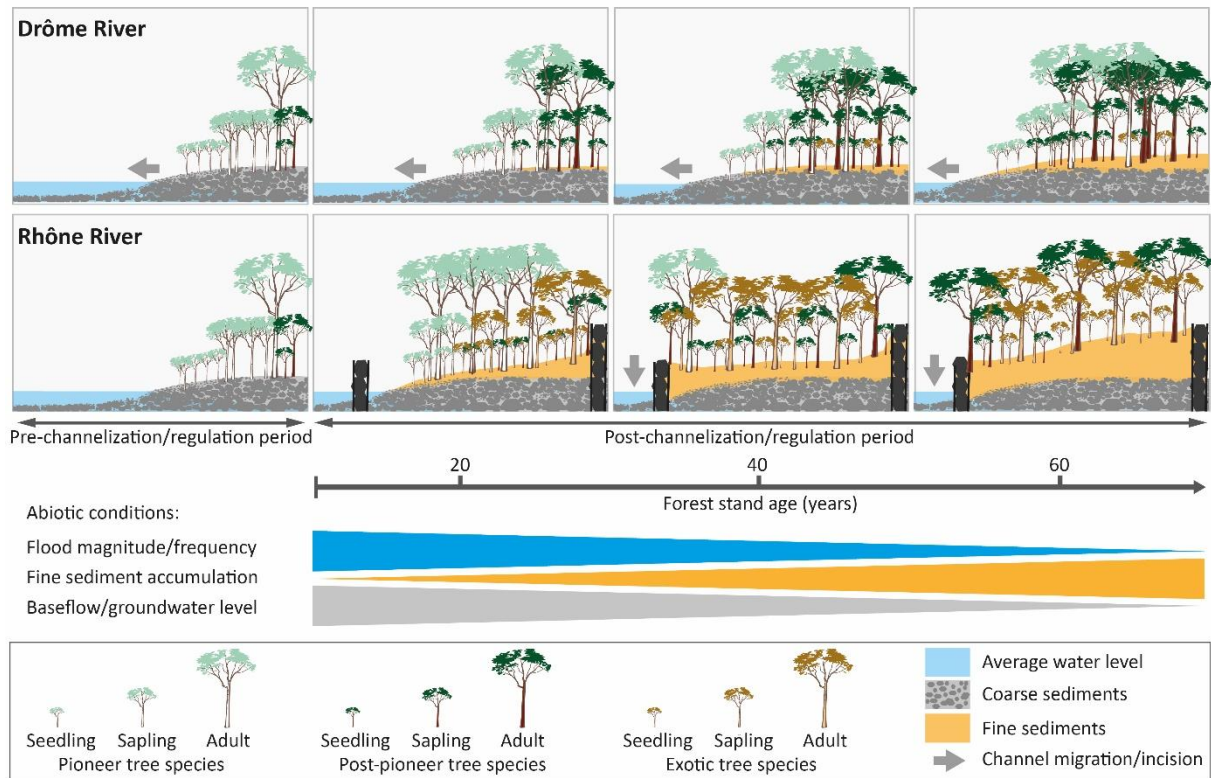


771 rivers Drôme and Rhône.

772 Figure 7. Constrained canonical analysis of principal coordinates of A) tree diameter classes and B) tree species  
 773 in riparian forests along the rivers Drôme and Rhône. To facilitate graphical interpretation, data are grouped  
 774 into three classes of forest stand age (<25, 25-50 and >50 years). In addition, the centroids in principle  
 775 coordinate space of the three most influential diameter classes ("70" is DBH > 70 cm; "52.5" is 51 cm < DBH <  
 776 56 cm; "12.5" is 11 cm < DBH < 16 cm) and tree species (*Acer.neg* is *Acer negundo*, *Sal.alb* is *Salix alba*, *Sam.nig*  
 777 is *Sambucus nigra*) are provided (see Appendix S9 and S10).



778 Figure 8. Conceptual model of ecological trajectory of riparian forests between the channelized and regulated  
 779 Rhône River and the relatively unmodified Drôme River, across a range of successional phases in eastern



780 France.