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**Long-term river management legacies strongly alter riparian forest attributes and constrain 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

## 1. Introduction

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

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

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

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

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

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

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

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

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

## **2. Material and Methods**

### **2.1. Study area**

The study was carried out along the Rhône River (total length = 810 km, catchment area = 96,500 km<sup>2</sup>, mean annual discharge = 1,700 m<sup>3</sup> s<sup>-1</sup>) in southeastern France (Figure 1). Comparable to other large rivers, the Rhône Basin has been subject to multiple uses since early settlement, including agriculture, forestry and gravel extraction. In the last two centuries, two extensive river engineering phases profoundly changed its course and its hydro-sedimentary and ecological functioning. During the 19th Century, an extensive system of longitudinal and lateral submersible stone dikes was constructed to aid river navigation in the main channel downstream of Lyon. The long chains of rectangular compartments, referred to as “dike fields”, concentrated the flow into a single-thread channel by damming secondary channels during low flows and fixing the position of pools and riffles. During the second half of the 20th Century following World War II, an ambitious program of economic recovery was initiated within the Rhône River corridor and a total of twenty-four dams and hydro-electric power plants were constructed. Of these, sixteen dams feature diversion canals, excavated in parallel to the natural river course, creating secondary bypass channels in these reaches (total length = 162 km, Lamouroux et al., 2015). The diversion dams distribute the largest part of the discharge into the canals, while the bypassed reaches receive only a minimum baseflow discharge (i.e., residual flow is 10 to 30% of the mean annual flow arriving at the upstream diversion dams) (Vázquez-Tarrío et al., 2019).

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



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

## 2.2. Dike field forest inventory

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

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

inventory and the measurement of environmental variables were done in spring 2014 within two nested concentric plot sizes: a 10-m radius plot (area: 314 m<sup>2</sup>) for recording all live and dead standing trees with a diameter at breast height (DBH)  $\geq$  7.5 cm, and a 20-m radius plot (area: 1,256 m<sup>2</sup>) for recording all live and dead standing trees with DBH  $\geq$  30 cm. Furthermore, three sub-plots of 1.5-m radius each (7 m<sup>2</sup>) were centered on the 10-m radius plot perimeter, positioned at due North and at 133 and 267 degrees radially, to inventory regeneration stems (i.e., DBH < 7.5 cm). For each tree, we recorded species, DBH and health class, comprising live trees (< 50% dead crown and branches), dying trees (>50% dead crown and branches), or dead trees.

To compare stand attributes between the study sites, data were standardized to a per hectare basis. Basal area (m<sup>2</sup> ha<sup>-1</sup>), mean diameter (cm) and stem density (stems ha<sup>-1</sup>) were calculated for total live standing trees, distinguishing between overstorey (i.e., DBH  $\geq$  7.5 cm) and understorey (i.e., DBH < 7.5 cm) vegetation and among pioneer, post-pioneer and exotic tree species (see Appendix 3 for details).

### **2.3. Environmental variables**

To assess conditions relative to the provision and accessibility of resources to the trees, as well as relative to the disturbance level, we measured fine sediment depth (median grain size  $\varnothing \leq$  2 mm) at each plot centre. We assumed that the fine grain-dominated material was deposited on top of coarse-grained material, which made up the former river channel or had accumulated in the initial phase following dike construction, when the dike field's connectivity to the main channel was still frequent. Using a soil corer ( $\varnothing =$  5 cm), we penetrated the ground until a dull sound and an increased resistance was perceived, which was assumed to reflect the gravel layer boundary, and measured that distance from the surface. To characterize the climatic gradient along the north-south Rhône River corridor, extending across a Continental to Mediterranean climate, we recorded the geographic coordinates (longitude and latitude) at the centre of each plot using a high-accuracy GPS (Trimble GEO7X). To describe the hydrological connectivity, we used two correlated variables (see Appendix 4 for correlation matrix), the relative surface elevation above the water level at a discharge of 100 m<sup>3</sup> s<sup>-1</sup>

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

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

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

## **2.5. Statistical analysis**

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

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

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

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

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

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

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

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

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

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

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

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

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

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

### **3. Results**

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

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

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

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

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

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

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

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

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

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

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

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

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



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

#### 4. Discussion

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

## **5. Conclusion**

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



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

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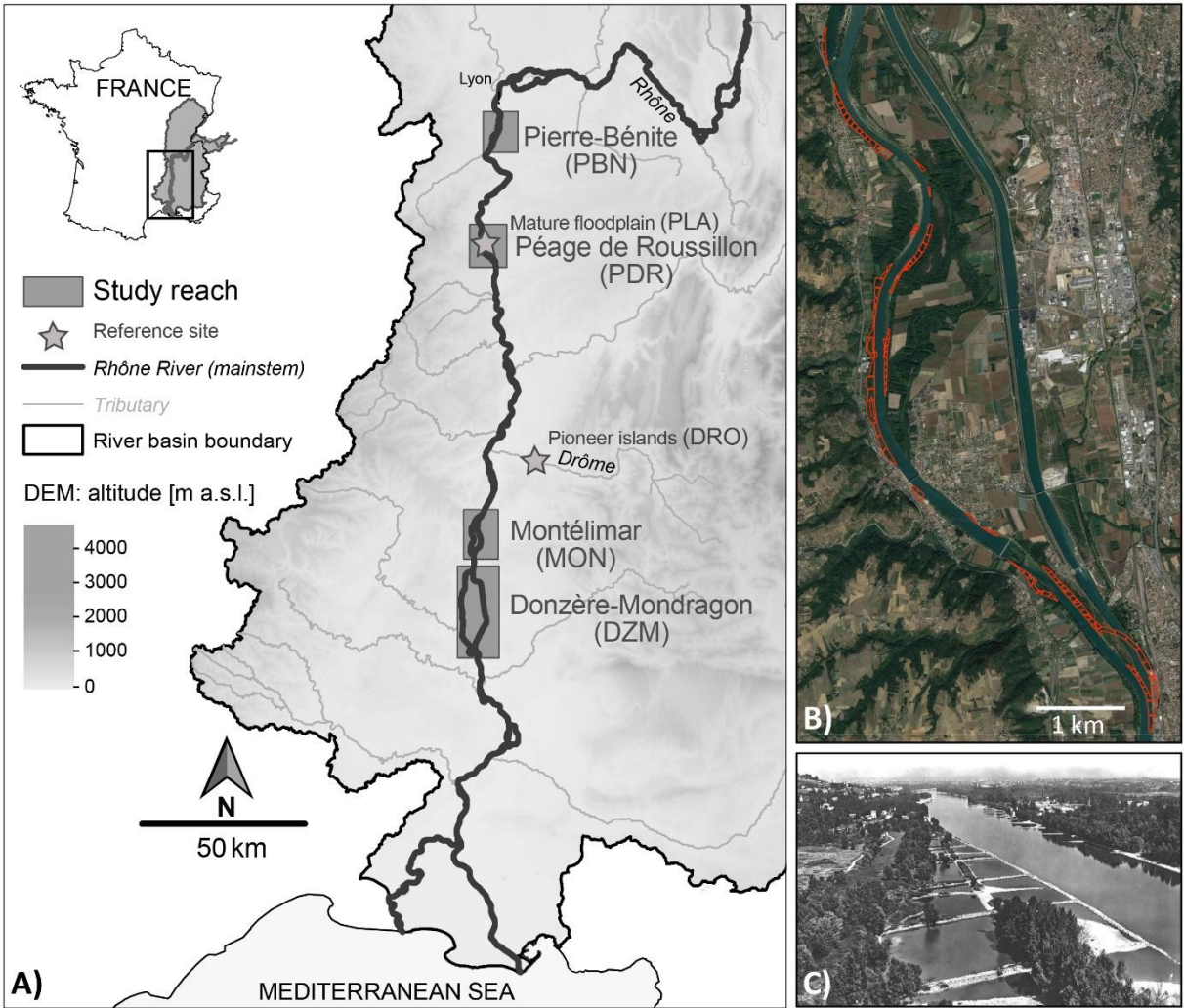
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809

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 <sup>-1</sup> )	- 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 <sup>2</sup> ha <sup>-1</sup> )	- 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 <sup>-1</sup> )	- 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 <sup>2</sup> ha <sup>-1</sup> )	- 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

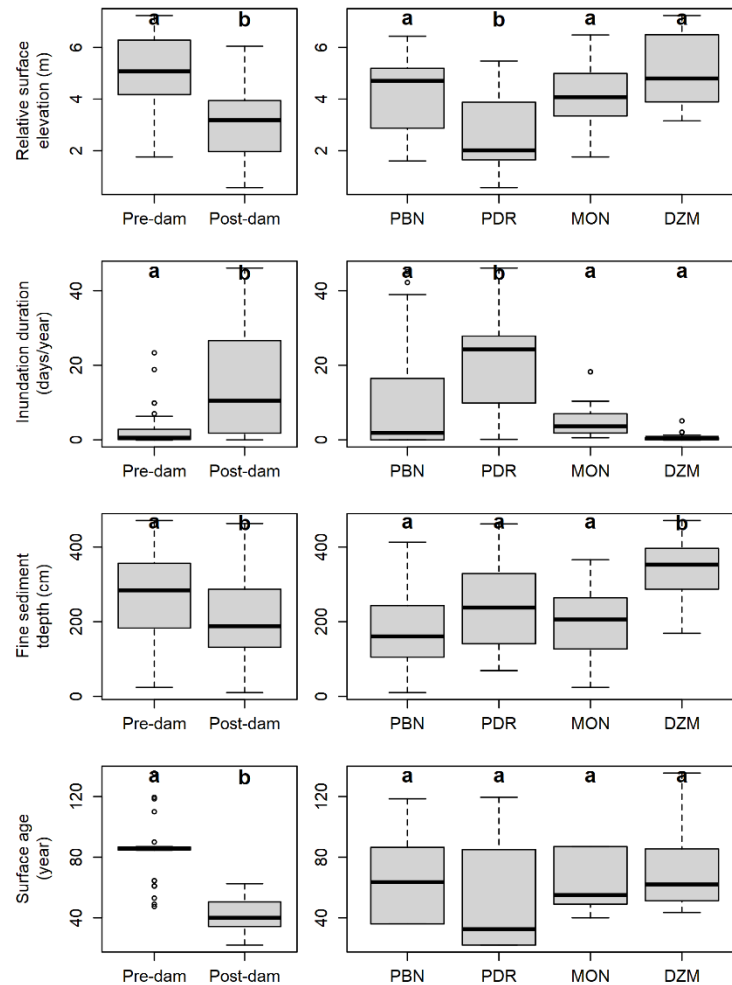
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**Figure 1.** Location of the four bypassed reaches studied along the Rhône River in southeastern France (A), distribution of the dike fields in the Péage de Roussillon bypassed reach (B, aerial photographs: Google Map) and detailed view of the dike fields early in the 20<sup>th</sup> century, before terrestrialization

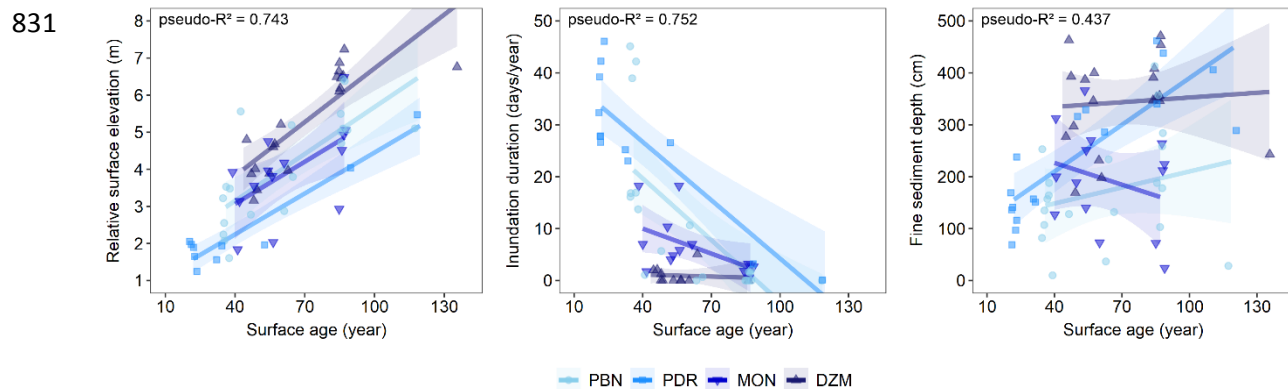


and afforestation (C, postcard: SMIRIL).

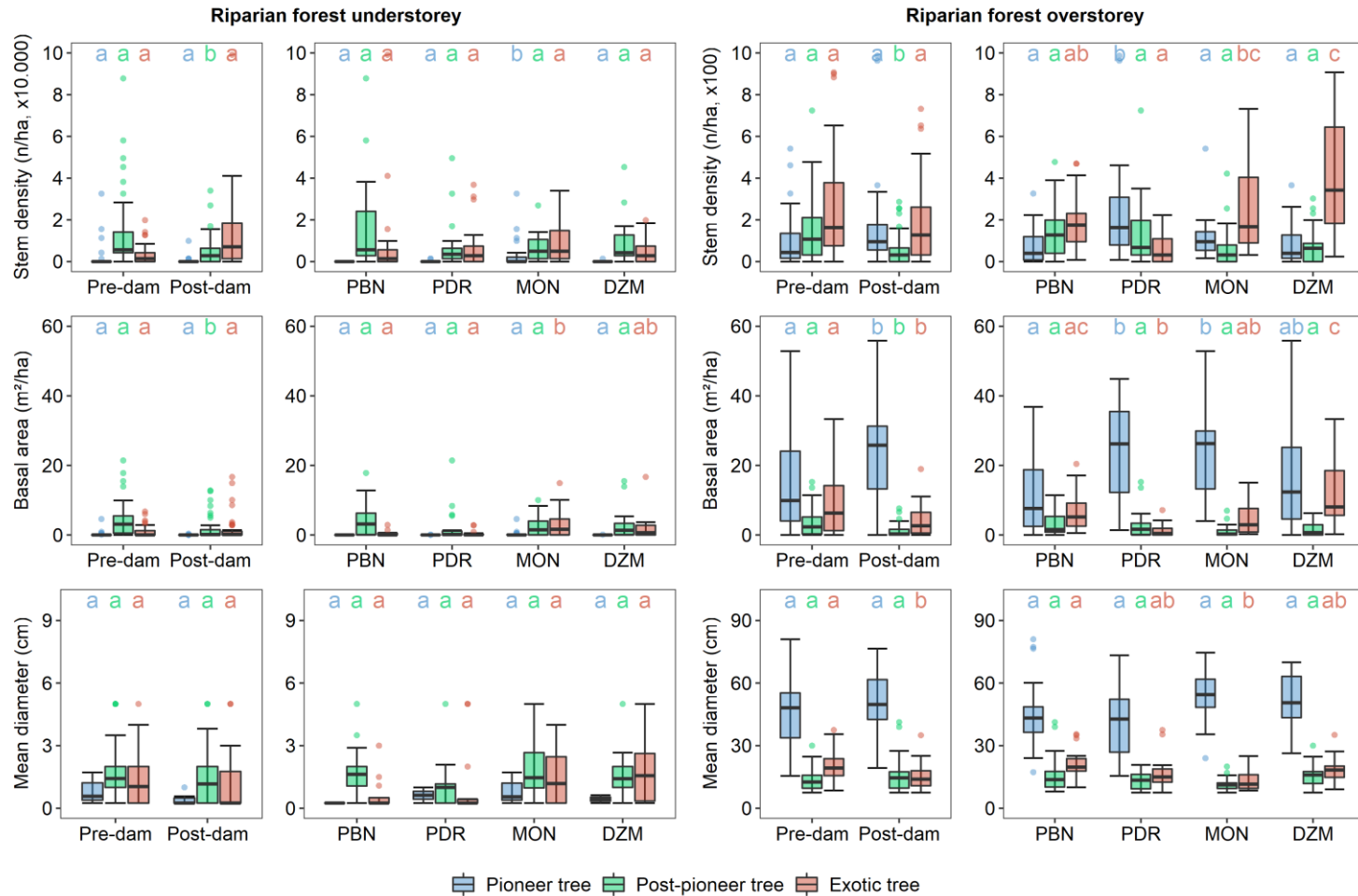
**Figure 2.** Variation in environmental variables between pre- and post-dam surfaces and bypassed reaches (PBN = Pierre-Bénite, PDR = Péage de Roussillon, MON = Montélimar, DZM = Donzère-Mondragon) on dike fields along the Rhône River, SE France. Boxplot with different letters indicate statistical significant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



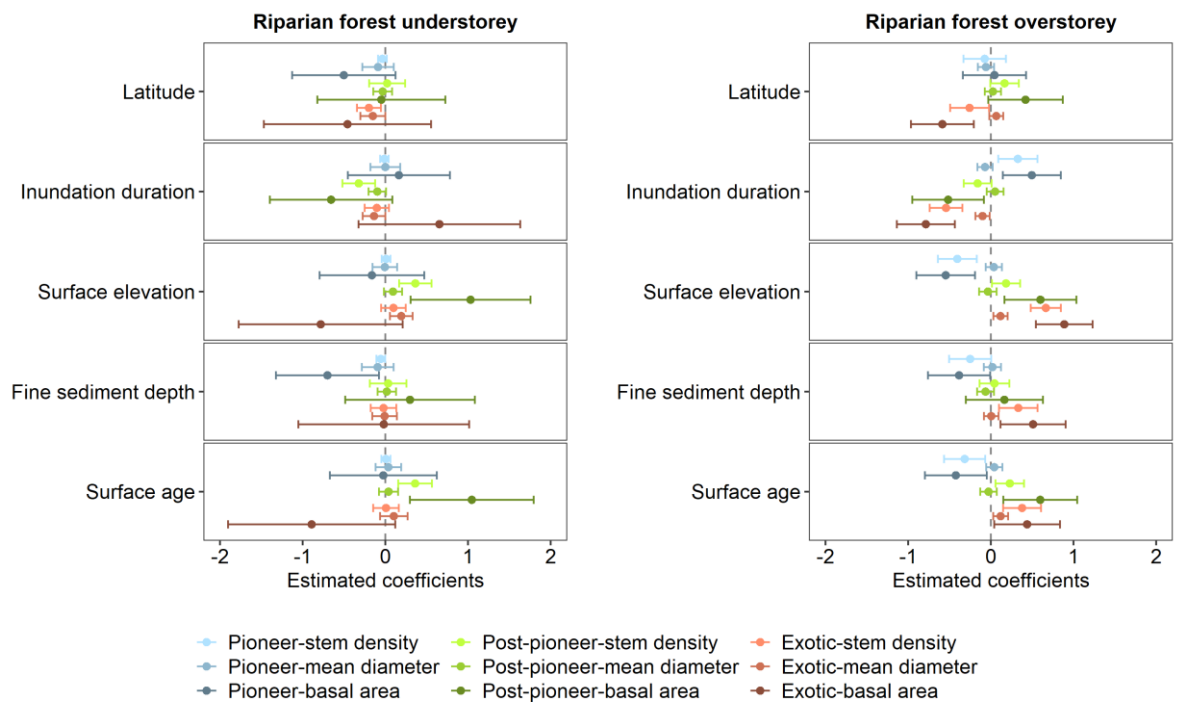
827 **Figure 3.** Variation in relative surface elevation , inundation duration and fine sediment depth at  
828 dike-field forest sites as a function of surface age along the Pierre-Bénite (PBN), Péage de Roussillon  
829 (PDR), Montélimar (MON) and Donzère-Mondragon (DZM) bypassed reaches of the Rhône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



832 **Figure 4.** Variations in understorey 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).



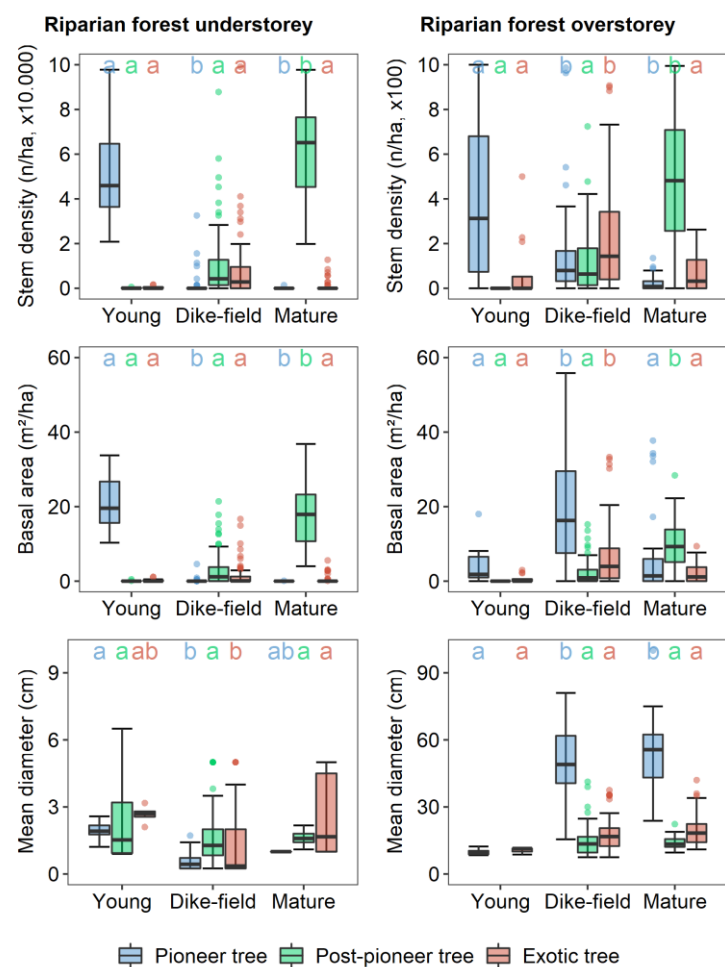
835 **Figure 5.** Average parameter estimates and 95% confidence intervals for environmental variables  
 836 used to predict variations in understorey and overstorey riparian forest attributes on dike fields along  
 837 the Rhône River, SE France (full model results are listed in Appendix 8 and detailed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

