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Long-term changes in the riparian vegetation of a large, highly anthropized river: Towards less hygrophilous and more competitive communities

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ABSTRACT

Vegetation resurvey has proven effective in understanding long-term trajectories of plant communities. Combined with information related to ecological preferences and ecological strategies of plants, this framework can provide insight into the dynamics of communities and associated ecological processes over several decades. By comparing old and recent vegetation surveys, we sought to understand how past changes in flow and sediment regimes along a 100-km reach of the Rhône river still influence the structure of riparian plant communities. Specifically, we studied variations in the mean and dispersion values of light, nutrient availability and soil moisture, as well as of competitors, stress tolerators and ruderals, at the community scale over four decades and along connectivity and productivity gradients. Results showed that communities were composed of more hygrophilous and heliophilous species in old surveys and that this decrease in soil moisture and light over time was broadly consistent along environmental gradients. In response to these environmental changes, the ecological strategies of riparian vegetation have evolved into more competitive and less stress-tolerant communities. This was illustrated by the decline of the pioneer species *Salix alba*, but the increase in several post-pioneer woody species. Given that these changes were observed on almost all the plots studied, irrespective of their position along the connectivity and productivity gradients, our results reflect to some extent an overall evolution of the system towards more mature and closed successional stages. Thus, over a period of 40-years, and probably due to the legacy effects of anthropogenic modifications to flow and sediment regimes that have favored more stable riparian environments, a directional shift of riparian communities towards more advanced successional stages was highlighted. In a context where past and present anthropogenic stressors are accumulating, we infer that these changes in riparian ecosystem properties are probably irreversible and represent a major challenge for restoration.

1. Introduction

In ecology, one of the main challenges of current research is to understand and anticipate the effects of anthropogenic changes on community assembly (Sutherland et al., 2013). However, because of lags in community response to environmental change (Jackson and Sax, 2010) but also because of contingency factors that can lead to divergence in the successional trajectories followed by communities (Clark et al., 2019), long-term studies are needed to understand the ecological processes that shape communities (Chang and HilleRisLambers, 2016). Indeed, repeated measurements of vegetation permanent plots over time have provided strong evidence of the influence of environmental changes on

community structure, but also of variation, often non-linear, in community response to global change (Bakker et al., 1996; de Bello et al., 2020). Nevertheless, these direct and regular observation rely on expensive and staff-intensive devices that are difficult to maintain over several decades. To overcome these challenges, but also to facilitate observational studies of plant dynamics over longer periods, the use of indirect approaches based either on chronosequences (Walker et al., 2010) or on the resurvey of historical plots (Hédil et al., 2017) has gained importance in ecology. Although these approaches have limitations related to spatial variation in historical sites trajectories in the first case (Johnson and Miyanishi, 2008) and to observation and relocation errors in the second case (Verheyen et al., 2018), overall they have proven to

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be effective in understanding shifts in community composition over long periods (Kapfer et al., 2017; Verheyen et al., 2017; Walker et al., 2010).

Beside changes in taxonomic composition, the use of information related to ecological preferences (Ellenberg et al., 1992), ecological strategies (Grime, 1977) and morphological traits (Westoby, 1998) of species have provided a framework for greater generalization of results through comparison of study areas characterized by different species pools (McGill et al., 2006). By integrating trait variation into long-term vegetation studies, it has thus been possible to demonstrate the consistency of succession patterns between widely different ecosystems (Rees et al., 2001). Applying to resurveys of historical plots, trait-based analyses can limit problems related to changes in observers between two dates and to the synonymy of species, because closely related species are expected to share many of the same traits (Freckleton et al., 2002). By combining historical plot resurveys with trait-based approaches, it is thus possible to conduct opportunistic studies that remobilize, e.g., old field notebooks, in order to make the best use of available data to understand the dynamics of plant communities and related ecological processes over long times. This has been successfully applied to understand changes in environmental conditions, approximated by Ellenberg values, in spring fens in response to 20th century acidification (Schweiger and Beierkuhnlein, 2017); variation in competitive, stress-tolerant and ruderal strategies of understorey communities in response to site fertility in boreal forest (Maliniemi et al., 2019); shifts in functional traits in semi-natural mountain grassland in response to decreased grazing intensity (Giarrizzo et al., 2017).

Here, we aimed to study the long-term changes of riparian plant communities, in terms of ecological preferences and strategies, by repositioning and resurveying numerous historical plots. Riparian communities occupy transitional zones between freshwater and terrestrial ecosystems and, in lotic environments, are subject to significant physical constraints, such as erosion and sedimentation processes, but also cyclic flooding and desiccation (Naiman and Decamps, 1997). These constraints induce strong variations in environmental conditions expressed by gradients in several spatial dimensions of the hydrosystem, from upstream to downstream, from the riverbed to the floodplain and from the water table to the substrate surface (Ward, 1989). In addition, due to temporal variations in flood intensity and frequency (Poff et al., 1997), which drive the disturbance dynamics of riparian zones, the successional trajectories of plant communities can be suddenly interrupted, with abrupt changes in abiotic conditions and vegetation composition (e.g., Dixon et al., 2015; Friedman and Lee, 2002; Greet et al., 2015). This allows the expression of a complex mosaic of habitats, more or less periodically rejuvenated, ranging from annual herbaceous communities on the gravel bars of the riverbed to aging forest stands on the floodplain (Junk et al., 1989), and explains why, relative to their narrow spatial extent in the landscape, riparian zones play a disproportionate ecological role (González et al., 2017).

To protect goods from flooding and to meet human needs for water and energy, most of the world's rivers have been regulated by dams and constrained by dikes (Belletti et al., 2020; Nilsson et al., 2001), with detrimental consequences for hydro-geomorphic processes (Poff et al., 2007). These anthropogenic modifications have profoundly altered the dynamics of riparian vegetation, simplifying communities (Aguar et al., 2018), increasing the representation of woody formations (Garófano-Gómez et al., 2013), especially exotic species (Janssen et al., 2020), and decreasing the representation of hygrophilous communities (Mikulová et al., 2020). To define effective conservation and restoration actions for degraded riparian zones, it is therefore essential to better understand the long-term response of plant communities to river adjustments caused by anthropogenic infrastructures. However, surprisingly few long-term studies of plant communities have been conducted in riparian zones (but see, Friedman et al., 2022; Johnson et al., 2012) and none have gone beyond taxonomic approaches. Indeed, to date, most studies have relied on the analysis of series of aerial photographs to characterise the temporal dynamics over several decades of riparian vegetation patches,

often limited to shrub and tree formations, in relation to changes in the hydrological regime (e.g., Geerling et al., 2006; Kui et al., 2017; Sanchis-Ibor et al., 2019; Sankey et al., 2015; Surian et al., 2015). Nevertheless, this approach is based on spatial units of observation that are too coarse to understand the processes that shape the succession trajectories of local communities. To address this research gap, but also to better understand the changes in ecological processes that shape riparian communities over time, in response to modifications in river flow and sediment regimes, we compared old and recent vegetation surveys along a regulated and channelized river reach of about 100 km. Specifically, we studied the variation in community-weighted mean values and functional dispersion values of Ellenberg indicators and Grime's CSR strategies along a connectivity and productivity gradients over a 40-year period by addressing the two following questions: (i) How do ecological requirements and ecological strategies of riparian plant communities vary between old and recent survey plots? (ii) Is the response of riparian plant communities to connectivity and productivity gradients different between old and recent survey plots?

2. Material and methods

2.1. Study area and experimental design

The study area is located in South-Eastern France along a reach of the Upper Rhône River (total length = 810 km, catchment area = 96,500 km²) and the lower valley of the Ain River (total length = 190 km, catchment area = 3,765 km²) (Fig. 1). The mean annual discharge varies between 420 (upstream part) and 600 (downstream part) m³.s⁻¹ for the Upper Rhône, and is 123 m³.s⁻¹ for the Ain River. This area is characterized by a temperate climate with monthly mean temperatures ranging from 3.0 to 21.2 °C and mean annual precipitation ranging from 870 mm (on the downstream part) to 1140 mm (on the upstream part).

The Upper Rhône River is a highly modified river, which has shifted from a braided pattern to a series of impounded reaches within the span of approximately one century (Olivier et al., 2009). To protect goods and people from flooding, this large river has been dammed along its entire length and, during the second half of the 20th century, a series of lateral canals (i.e., diversion canal), running parallel to the natural Rhône River channel (i.e., by-passed reach), was built to produce hydropower and facilitate irrigation and navigation (for further details see, Appendix S1). In the eastern (Miribel-Jonage) and western (Bregnier-Cordon) parts of the study area, two hydroelectric complexes convey a large part of the river flow into the diversion canal and limit the level of flow release to 30–60 m³/s in the Miribel-Jonage by-passed reach and 80–160 m³/s in the Bregnier-Cordon by-passed reach. These developments have greatly altered the flow and sediment regimes of the Rhône and have induced channel incision, lateral stabilization and armouring of the channel bed, with consequences for riparian vegetation (Bravard et al., 1986; Petit et al., 1996). The Ain River is regulated by a series of five dams in its upstream section, built in the first half of the 20th century, which triggered a shift from a braided to a free meandering channel in its downstream section (Marston et al., 1995). This unconstrained river have also experienced channel incision and channel narrowing since the second half of the 20th century, mostly due to gravel mining in the floodplain and afforestation in the watershed (Liébault and Piégay, 2002).

Beyond these general characteristics, significant differences in bedload properties and functioning exist between the western and eastern parts of the study area. The western part, i.e., the lower Ain Valley, the confluence with the Rhône and the Miribel-Jonage by-passed reach, is characterized by a dominance of gravels and pebbles with still active bedload transport capacities of coarse sediments (Petit et al., 1996; Vázquez-Tarrio et al., 2019). The eastern part, i.e., the upstream reach at the Ain-Rhône confluence and the Brégnier-Cordon by-passed reach, is characterized by a dominance of sands and silts with a mobility limited to the fine fraction. This spatial configuration contributes to the

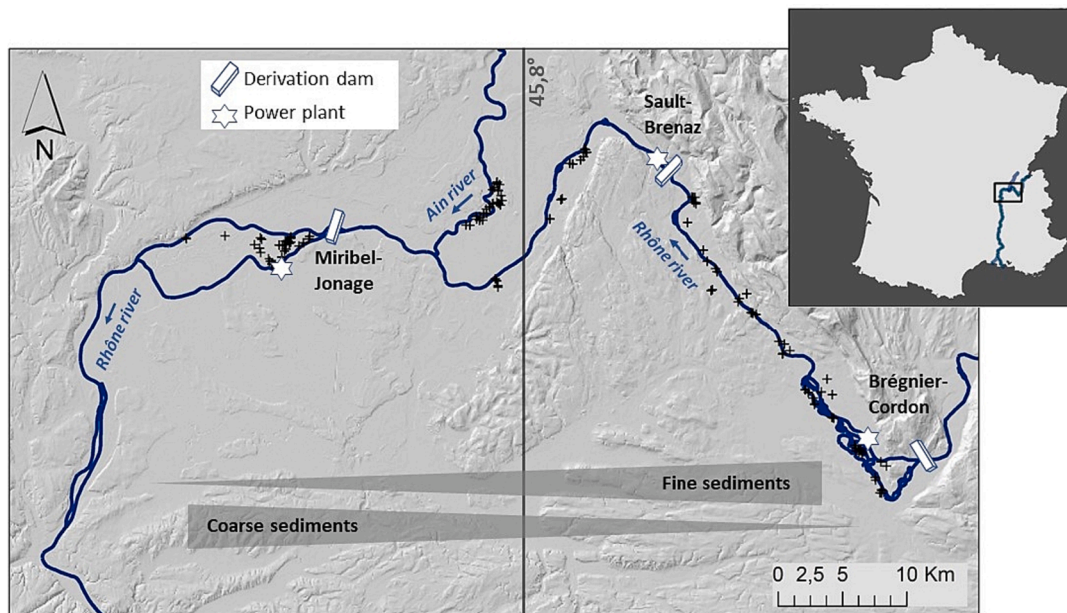


Fig. 1. Location of the study area within the Rhône River watershed, distribution of the survey plots along the Upper Rhône and Ain rivers (+).

establishment of a longitudinal environmental gradient opposing in the eastern part of the study area more fertile and humid edaphic conditions and in the western part more dry and stressful edaphic conditions.

2.2. Vegetation surveys

Several floristic survey campaigns were performed in the study area between 1980s and 1990s (Bravard et al., 1986; Marston et al., 1995; Pautou et al., 1992). Among them, we gathered 171 old plots corresponding to different EUNIS habitat types: *Phalaris arundinacea* beds (C3.26); sparsely vegetated river gravel banks (C3.55); sub-Atlantic semi-dry calcareous grassland (E1.26); central European calcareous grassland (E1.28); riverine *Salix* woodland (G1.11); riverine *Fraxinus - Alnus* woodland, wet at high but not at low water (G1.21); mixed *Quercus - Ulmus - Fraxinus* woodland of great rivers (G1.22). Of these, 76 old plots were derived from field survey books conducted as part of phytosociological surveys (J. Girel, unpublished data), whose location was marked on printed topographic maps (1:25,000) that were digitized in a GIS (ArcGIS 10.7.1 Esri Inc.). The others 95 old plots were extracted from a regional floristic database (<https://www.biodiversite-auvergne-rhone-alpes.fr/pifh>) for which geographical coordinates in latitude and longitude, were provided. We then used a series of aerial photographs, taken from 1979 to 1986 for old series, and from 2015 to 2020 for recent series, to eliminate old survey plots where significant land use change occurred. The final dataset consisted of 118 old survey plots distributed throughout the study area (Fig. 1) and representing main riparian habitats. These old plots, although not permanently marked, had a reliable approximate location and can thus be considered “quasi-permanent” plots (Kapfer et al., 2017).

Based on the locations translated into geographic coordinates of old survey plots, recent survey plots were carried out in late spring (end of May to June) in 2020 and 2021 using the same methodology. They were relocated using a centimetric-accurate GPS receiver (©GNSS Trimble R2). For each recent plot, plants communities were sampled in quadrats of comparable size to the original old plots, i.e., from 50–100 m² for herbaceous vegetation to 400–800 m² for forest stands; and plant species cover was recorded using the Braun-Blanquet method. However, because species cover data were not available for the old plots, subsequent analyses were performed considering presence/absence data. Finally, to limit observer biases, all recent surveys were performed by

the first author (VB).

2.3. Species ecological preferences and strategies

To analyse how the ecological preferences and ecological strategies of riparian plants varied between old and recent surveys, as well as with environmental conditions, we collected data for each species from two sources of information (Appendix S2). Ellenberg’s indicator values (Ellenberg et al., 1992) for light (L), nutrient availability (N) and soil moisture (F) were extracted from the Baseflor database (Julve, 1998) and used to characterize variations in habitat preferences of species. Among the 448 species encountered, these values were unavailable for two species, one with a single occurrence in our data set (i.e., singleton species) and one identified at the genus level. Grime’s values (Grime, 1977) for respectively Competitors, Stress tolerators and Ruderals, i.e. ternary coordinates, were extracted from the list of species available in Pierce et al. (2017) and used to characterize variations in the strategy–environment relationships of riparian plants. For missing values (n = 92), data were either completed by using ecological information on closely related species, i.e., for the same genus (n = 81), or discarded (singleton species, n = 9; others, n = 4).

At the scale of each quadrat, we then computed the community-weighted means (CWM) and the functional dispersion (FDIs) for each ecological preferences and ecological strategies value (FD package, Laliberté et al., 2014). CWM is defined as the mean value weighted by the relative cover of each species bearing each value (Lavorel et al., 2008) and FDis is defined as the mean distance of individual species to the weighted centroid of all species in the assemblage (Laliberté and Legendre, 2010).

2.4. Environmental data

At the centre of each quadrat of the recent survey plots, the coordinates (longitude, latitude and altitude) were measured using a GPS receiver with centimetric accuracy. From these measurements, the elevation difference and distance from the centre of the main riverbed, used hereafter as connectivity parameters, were characterized in a GIS (ArcGIS 10.7.1 Esri Inc.). First, we determined for each plot the position of the nearest point located on main stream bed of the Rhône or Ain River (from the Carthage® database) and then calculated the

distance between the center of the plot and this point. Second, we extracted from a Digital Elevation Model (RGE alti®, 5 m resolution) the elevation of the plot and the elevation of the nearest main stream bed point and determined the elevation difference by subtracting these two values. Soil properties, use hereafter as productivity parameters, were characterized using a soil corer in the centre of each quadrat to describe the soil texture classes, based on [Jamagne's \(1967\)](#) texture triangle, and estimated the thickness of fine sediments (silt). The percentage of sand was derived by keeping the central value of each of the triangle texture classes and the sediment thickness by measuring the distance from the surface to the interface with the gravel layer.

2.5. Statistical analysis

The continuous independent variables were the longitude (denoted 'Longitude' in tables and figures), the elevation difference ('Elevation') and distance to riverbed centre ('Distance'), the thickness ('Thickness') of fine sediments and the proportion of sand ('Texture') (See Appendix S3 for correlation matrix). The independent factor was the date of surveys ('Date', two-level factor). Prior to analysis, a logit transformation was applied to the proportional variable 'Texture'. Also, because independent variables were measured on different scales and because we were interested in interpreting the main effects of continuous variables in the presence of interactions, all input variables were scaled ([Schielezth, 2010](#)). Dependent variables were the CWM and the FDis of values of ecological preferences (Ellenberg' values) and ecological strategies (Grime' values) of riparian species at the community scale (i.e., quadrat).

To determine whether the mean and dispersion values of ecological preferences and ecological strategies of riparian communities varied between old and recent surveys, we used paired *t*-test (stats package). As multiple comparison tests were performed, we adjusted the *p* values with the Benjamini and Hochberg correction.

To determine how environmental conditions explained differences in the mean and dispersion values of ecological preferences and ecological strategies of riparian communities between old and recent surveys, we used a modelling approach. We considered a set of 9 a priori models (Appendix S4), testing additive and interactive effects between 4 environmental variables (connectivity and soil parameters) and the date of survey. Since we knew that the position of the quadrat along the longitudinal gradient of the Rhône River significantly influenced several dependent variables, we included 'Longitude' as a covariate in all a priori models. We then fitted linear models with a Normal distribution to each dependent variables and used the Akaike's information criterion corrected for small sample sizes to identify the most parsimonious model. The goodness of fit of each model was estimated using the adjusted coefficient of determination. In all candidate models, the variance inflation factor was below three, indicating a lack of collinearity issues ([Dormann et al., 2013](#)). To estimate parameters and associated unconditional standard errors, we performed model averaging based on all a priori models (MuMin package, [Barton, 2015](#)).

To determine individual species response to time spent between the two surveys (old vs recent), we used indicator species analysis (indicspecies package, [De Cáceres and Legendre, 2009](#)), based on the indicator values index (IndVal). Low-frequency species (occupying < 10 % of the sites) and high-frequency species (occupying > 90 % of the sites) species were discarded (*n* = 403) and a permutation test (*n* = 9999) was applied to test for the statistical significance of indicator species.

Analyses were performed with R version 4.0.0 ([R Core Team, 2020](#)).

3. Results

A total of 448 species (mean ± SD = 18 ± 7) were recorded in the 236 quadrats along the Upper Rhône and Ain rivers. Of these, 373 species (mean ± SD = 17 ± 9) were recorded in the 118 older quadrats and 303 species (mean ± SD = 19 ± 5) in the 118 recent quadrats.

3.1. Variations in the mean and dispersion values of ecological preferences and ecological strategies of communities between old and recent surveys

Paired *t*-test showed that the mean values for light and soil moisture, as well as for stress-tolerators, decreased significantly between old and recent surveys while the mean value for competitors increased significantly ([Table 1](#)). In addition, the dispersion value for soil moisture decreased significantly between old and recent surveys while the dispersion values for light, as well as for stress-tolerators and ruderals increased significantly.

3.2. Variations in the mean values of ecological preferences and ecological strategies of communities along environmental gradients between old and recent surveys

Linear models showed that models including soil variables ranked first for most dependent variables, while models including connectivity variables ranked first for the mean value of soil moisture and ruderals ([Table 2](#) & detailed results in Appendix S5). Model averaging revealed that only the mean value for stress-tolerators and ruderals were significantly influenced by the interaction between the distance to riverbed and survey date ([Table 3](#)). Graphical interpretation showed that communities established close to the riverbed were more stress-tolerant but less ruderals in older surveys than in recent ones ([Figs. 2 & 3](#)). In addition, the mean value for soil moisture decreased significantly with increasing elevation from the riverbed and the increasing proportion of sand in soil. The mean value for light decreased significantly with increasing fine sediment thickness but increased significantly with increasing proportion of sand in soil, while the mean value for nutrient availability showed exactly opposite patterns. With regard to ecological strategies, the mean value for competitors decreased significantly with increasing elevation and distance to the riverbed, as well as with increasing proportion of sand in the soil, but increased significantly with increasing fine sediment thickness. Finally, the mean value for ruderals increased significantly with increasing elevation to the riverbed and with increasing proportion of sand in the soil.

3.3. Variations in the dispersion values of ecological preferences and ecological strategies of communities along environmental gradients between old and recent surveys

Linear models showed that models including connectivity variables best-explained changes in the dispersion values of soil moisture, stress-tolerators and ruderals, while models including soil variables best-explained changes in the dispersion values of light, nutrient availability and competitors ([Table 2](#) & detailed results in Appendix S5). Model averaging revealed that only the dispersion values for nutrient availability and ruderals varied significantly with the distance to riverbed and survey date ([Table 4](#)). Graphical interpretation showed that dispersion values for nutrient availability far to the riverbed were higher in older than in recent surveys, but that dispersion values for ruderals close to the riverbed were higher in recent than in older surveys ([Figs. 4 & 5](#)). In addition, the dispersion values for soil moisture decreased significantly with increasing elevation from the riverbed, the dispersion values for light increased significantly with increasing fine sediment thickness and the dispersion values for nutrient availability increased significantly with increasing elevation from the riverbed and increasing proportion of sand in soil but decreased significantly with increasing fine sediment thickness. With regard to ecological strategies, the dispersion values of competitors decreased significantly with increasing fine sediment thickness, the dispersion values of stress-tolerators and ruderals increased significantly with increasing elevation from the riverbed and the dispersion values of ruderals increased significantly with increasing proportion of sand in soil.

Table 1

Variations in the mean (CWM) and dispersion (FDis) values of ecological preferences (Ellenberg' values) and ecological strategies (Grime' values) of riparian communities between old and recent surveys, along the upper Rhône and Ain rivers, France (*t*-value and *p*-value based on paired *t*-test).

Variables		Old		Recent		<i>t</i> -value	<i>P</i>	Adjusted <i>p</i>
		Mean (±SD)	Range	Mean (±SD)	Range			
Mean value	Soil moisture	5.49 (±1.29)	3.14–8.67	5.20 (±0.94)	3.00–8.88	3.652	0.000	0.001
	Light	6.85 (±0.67)	5.43–8.14	6.58 (±0.65)	5.45–8.18	6.206	0.000	0.000
	Nutrient	5.11 (±1.13)	2.50–6.92	5.23 (±1.05)	2.41–7.18	−1.580	0.117	0.140
	Competitive	31.55 (±7.77)	11.92–52.81	33.28 (±6.74)	17.22–47.08	−3.140	0.002	0.004
	Stress-tolerant	41.55 (±9.13)	21.65–65.38	38.78 (±7.04)	22.51–63.53	3.289	0.001	0.003
	Ruderal	26.91 (±8.38)	5.21–47.84	27.94 (±5.68)	16.98–43.51	−1.337	0.184	0.200
Dispersion value	Soil moisture	0.60 (±0.16)	0.22–1.01	0.54 (±0.16)	0.17–0.94	3.209	0.002	0.003
	Light	0.62 (±0.19)	0.19–1.14	0.68 (±0.16)	0.38–1.08	−3.611	0.000	0.001
	Nutrient	0.59 (±0.20)	0.28–1.12	0.57 (±0.16)	0.27–0.98	1.747	0.083	0.111
	Competitive	0.67 (±0.17)	0.31–1.20	0.65 (±0.13)	0.36–0.98	1.263	0.209	0.209
	Stress-tolerant	0.76 (±0.16)	0.25–1.19	0.80 (±0.12)	0.52–1.20	−2.544	0.012	0.018
	Ruderal	0.62 (±0.19)	0.19–1.15	0.70 (±0.15)	0.36–1.17	−3.786	0.000	0.001

3.4. Response of individual species to time spent between the two surveys

Indicator species analysis revealed that, among the 45 species considered, two were significantly characteristic of old surveys: *Salix alba* (IndVal = 0.409, *p* = 0.004) and *Hypericum perforatum* (IndVal = 0.353, *p* = 0.033). On the other hand, 17 species were significantly characteristic of recent surveys: *Ligustrum vulgare* (IndVal = 0.662, *p* = 0.001), *Hedera helix* (IndVal = 0.657, *p* = 0.001), *Crataegus monogyna* (IndVal = 0.627, *p* = 0.005), *Dioscorea communis* (IndVal = 0.618, *p* = 0.001), *Cornus sanguinea* (IndVal = 0.602, *p* = 0.002), *Fraxinus excelsior* (IndVal = 0.599, *p* = 0.001), *Rubus fruticosus* (IndVal = 0.515, *p* = 0.001), *Rubus caesius* (IndVal = 0.508, *p* = 0.001), *Corylus avellana* (IndVal = 0.481, *p* = 0.024), *Brachypodium sylvaticum* (IndVal = 0.465, *p* = 0.001), *Viburnum lantana* (IndVal = 0.481, *p* = 0.024), *Lonicera xylosteum* (IndVal = 0.443, *p* = 0.007), *Clematis vitalba* (IndVal = 0.440, *p* = 0.001), *Ulmus minor* (IndVal = 0.434, *p* = 0.004), *Galium aparine* (IndVal = 0.407, *p* = 0.001), *Prunus mahaleb* (IndVal = 0.376, *p* = 0.001) and *Acer campestre* (IndVal = 0.374, *p* = 0.014).

4. Discussion

Worldwide, human activities have transformed and impacted the functioning of most terrestrial ecosystems (Ellis et al., 2010). The long-term influences of anthropogenic stressors have been demonstrated on many ecosystems (e.g., Giarrizzo et al., 2017; Maliniemi et al., 2019; Schweiger and Beierkuhnlein, 2017), with legacy effects still acting on communities sometimes hundreds of years after the pressures have ceased (Dupouey et al., 2002). Here, using vegetation resurvey, we

showed that more than 40 years after the flow and sediment regimes of the Rhône and Ain rivers were modified by dams, riparian vegetation is still adapting to the new environmental conditions. More specifically, we have highlighted a general evolution of the system towards less humid and less luminous environmental conditions and towards more competitive and less stress-tolerant plant communities. This indicated that the legacy effects of anthropogenic modifications due to flow and sediment regimes have promoted more stable riparian environments which enabled the succession to progress to more mature, closed stages. These findings, based on a direct assessment of the temporal response of plant communities, complement other studies based on old aerial photos (e.g., Janssen et al., 2021), and reveal the long-term impacts that anthropogenic developments have on rivers and associated riparian vegetation.

4.1. The riparian environment has evolved to less hygrophilic and more sciaphilic conditions

Overall, in 40 years, the mean value for soil moisture in riparian plant communities has decreased as well as the co-occurrence of xerophilous and hygrophilous species. These changes revealed that the communities were composed of more hygrophilous species in old surveys and that, over time, many of these species have disappeared. This change is well illustrated by the significant decrease in the presence of white willow, *Salix alba*, on the studied reach of the Rhône and Ain River between the old and recent surveys. As documented for other *Salix* species (Rodríguez-González et al., 2017), the regeneration of this pioneer species related to alluvial bars has proven to be vulnerable to

Table 2

Top ranking models predicting variations in the mean (CWM) and dispersion (FDis) values of ecological preferences (Ellenberg' values) and ecological strategies (Grime' values) of riparian communities along the Upper Rhône and Ain River, France, as assessed with the Akaike information criterion corrected for small sample size (AICc). Number of estimated parameters including the intercept (*k*), AICc value, AICc weight (*W*) and marginal coefficient of determination (*R*²) are provided (for detailed results, please see Appendix S5).

Variables		Candidate model	<i>k</i>	AICc	<i>W</i>	<i>R</i> ²
Mean value	Soil moisture	Longitude + Date * Elevation	6	627.6	0.617	0.368
	Light	Longitude + Date + Thickness	5	333.7	0.718	0.479
	Nutrient	Longitude + Date + Thickness	5	606.5	0.740	0.374
	Competitive	Longitude + Date + Thickness	5	1521.8	0.660	0.326
	Stress-tolerant	Longitude + Date + Thickness	5	1644.2	0.440	0.112
	Ruderal	Longitude + Date * Distance	6	1577.6	0.954	0.115
Dispersion value	Soil moisture	Longitude + Date + Elevation	5	−214.8	0.598	0.162
	Light	Longitude + Date + Thickness	5	−208.9	0.730	0.249
	Nutrient	Longitude + Date + Texture	5	−236.4	0.272	0.383
	Competitive	Longitude + Date + Thickness	5	−284.7	0.496	0.213
	Stress-tolerant	Longitude + Date + Elevation	5	−270.3	0.551	0.120
	Ruderal	Longitude + Date + Elevation	5	−179.3	0.631	0.120

Table 3

Estimate coefficients (Estimate (±SE)) and confidence intervals (95 % CI) for each variable used to predict variations in the mean (CWM) values of ecological preferences (Ellenberg' values) and ecological strategies (Grime' values) of riparian communities along the Upper Rhône and Ain River, France. The 95 % confidence interval of coefficients in bold excluded 0.

Parameters	Soil moisture (CWM)		Light (CWM)		Nutrient (CWM)	
	Estimate (±SE)	(95 % CI)	Estimate (±SE)	(95 % CI)	Estimate (±SE)	(95 % CI)
Longitude	0.463 (±0.065)	(0.335; 0.590)	-0.285 (±0.035)	(-0.354; -0.217)	0.443 (±0.062)	(0.320; 0.565)
Date	-0.295 (±0.118)	(-0.526; -0.064)	-0.272 (±0.063)	(-0.397; -0.148)	0.120 (±0.113)	(-0.101; 0.342)
Elevation	-0.396 (±0.094)	(-0.580; -0.211)	0.022 (±0.043)	(-0.062; 0.105)	-0.140 (±0.080)	(-0.296; 0.016)
Distance	-0.112 (±0.083)	(-0.275; 0.052)	-0.015 (±0.051)	(-0.114; 0.085)	-0.094 (±0.083)	(-0.256; 0.068)
Thickness	0.094 (±0.077)	(-0.056; 0.245)	-0.241 (±0.039)	(-0.319; -0.164)	0.352 (±0.069)	(0.217; 0.487)
Texture	-0.217 (±0.086)	(-0.386; -0.049)	0.167 (±0.042)	(0.084; 0.250)	-0.211 (±0.078)	(-0.365; -0.058)
Date*Elevation	0.204 (±0.118)	(-0.028; 0.435)	-0.001 (±0.070)	(-0.138; 0.136)	0.111 (±0.120)	(-0.125; 0.346)
Date*Distance	0.100 (±0.125)	(-0.144; 0.345)	0.085 (±0.070)	(-0.052; 0.222)	-0.114 (±0.120)	(-0.350; 0.121)
Date*Thickness	-0.048 (±0.125)	(-0.293; 0.197)	-0.030 (±0.064)	(-0.155; 0.094)	0.012 (±0.113)	(-0.210; 0.235)
Date*Texture	0.135 (±0.123)	(-0.106; 0.377)	0.029 (±0.067)	(-0.103; 0.160)	0.098 (±0.119)	(-0.135; 0.331)

Parameters	Competitive (CWM)		Stress-tolerant (CWM)		Ruderal (CWM)	
	Estimate (±SE)	(95 % CI)	Estimate (±SE)	(95 % CI)	Estimate (±SE)	(95 % CI)
Longitude	2.289 (±0.433)	(1.440; 3.138)	-1.423 (±0.652)	(-2.700; -0.146)	-0.408 (±0.509)	(-1.405; 0.590)
Date	1.730 (±0.786)	(0.190; 3.270)	-2.772 (±1.018)	(-4.768; -0.776)	1.035 (±0.883)	(-0.695; 2.765)
Elevation	-1.075 (±0.525)	(-2.104; -0.046)	-0.452 (±0.632)	(-1.690; 0.787)	1.520 (±0.561)	(0.419; 2.620)
Distance	-1.348 (±0.529)	(-2.385; -0.310)	-1.892 (±0.838)	(-3.534; -0.250)	3.176 (±0.714)	(1.777; 4.575)
Thickness	2.507 (±0.516)	(1.495; 3.520)	-1.368 (±0.754)	(-2.845; 0.109)	-1.039 (±0.597)	(-2.209; 0.131)
Texture	-1.929 (±0.504)	(-2.917; -0.940)	0.500 (±0.677)	(-0.828; 1.827)	1.432 (±0.598)	(0.259; 2.605)
Date*Elevation	0.453 (±0.840)	(-1.194; 2.100)	-0.072 (±1.042)	(-2.113; 1.970)	-0.374 (±0.910)	(-2.158; 1.410)
Date*Distance	-0.282 (±0.834)	(-1.917; 1.353)	2.821 (±1.024)	(0.814; 4.829)	-2.546 (±0.884)	(-4.278; -0.814)
Date*Thickness	0.685 (±0.787)	(-0.859; 2.228)	-1.424 (±1.018)	(-3.419; 0.572)	0.748 (±0.920)	(-1.055; 2.550)
Date*Texture	-0.062 (±0.818)	(-1.665; 1.542)	0.774 (±1.039)	(-1.263; 2.810)	-0.712 (±0.913)	(-2.502; 1.078)

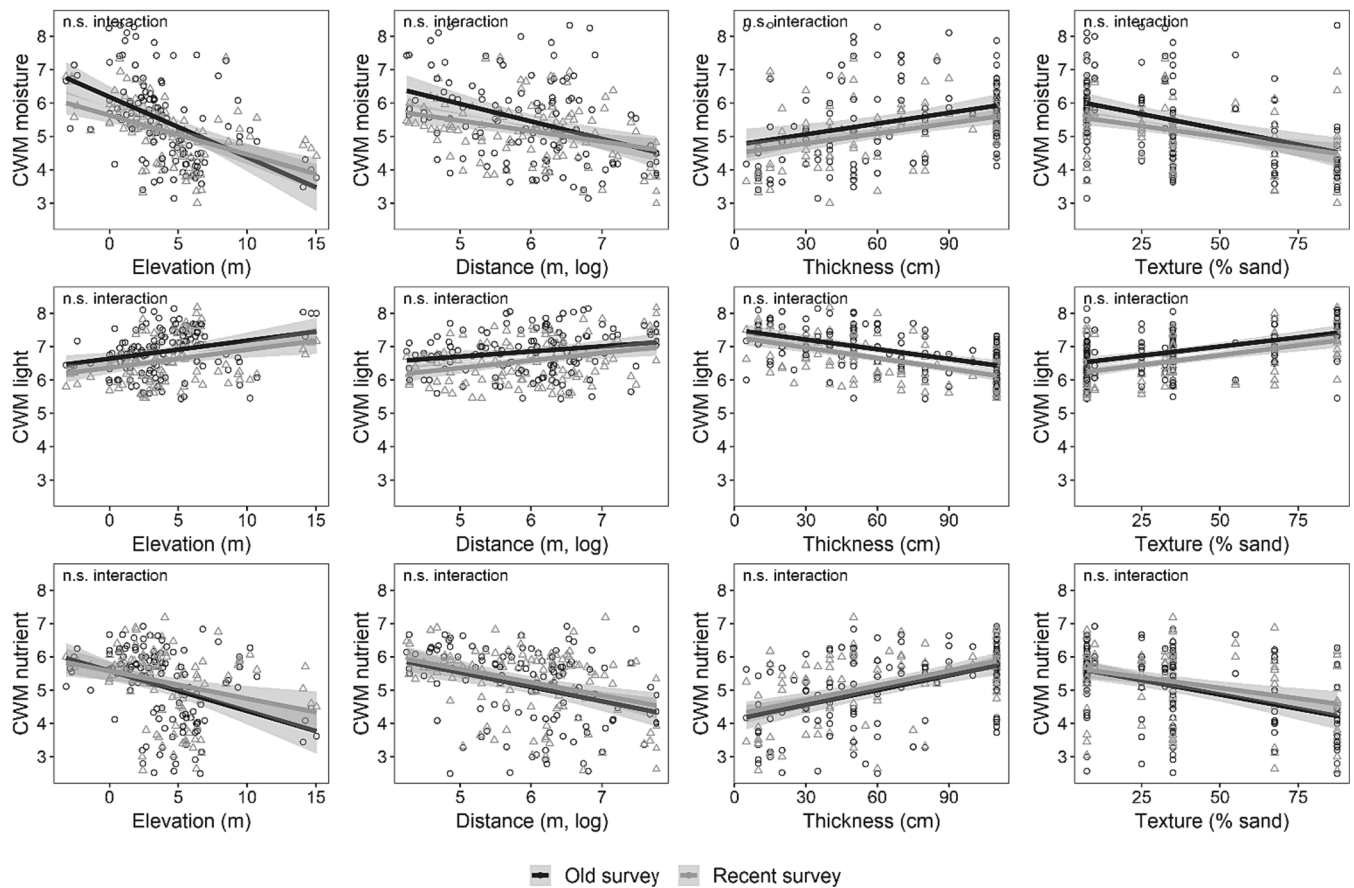


Fig. 2. Variation in the mean (CWM) values of ecological preferences (Ellenberg' values) of riparian communities with connectivity and soil variables between the old and recent surveys, along the Upper Rhône and Ain rivers, France (n.s. interaction = non-significant environmental variable × Date interaction).

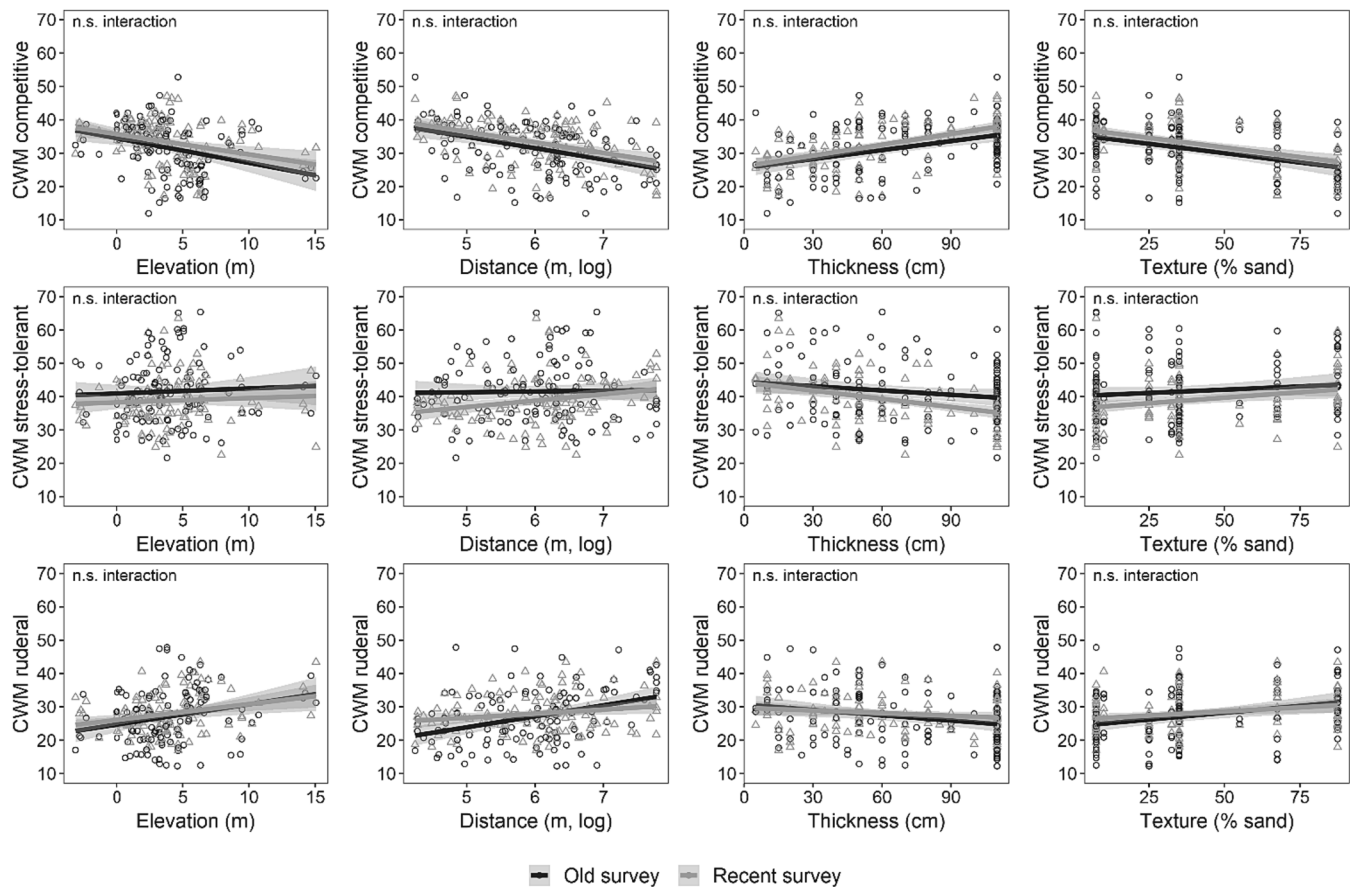


Fig. 3. Variation in the mean (CWM) values of ecological strategies (Grime' values) of riparian communities with connectivity and soil variables between the old and recent surveys, along the Upper Rhône and Ain rivers, France (n.s. interaction = non-significant environmental variable × Date interaction).

Table 4

Estimate coefficients (Estimate (±SE)) and confidence intervals (95 % CI) for each variable used to predict variations in the dispersion (FDis) values of ecological preferences (Ellenberg' values) and ecological strategies (Grime' values) of riparian communities along the Upper Rhône and Ain River, France. The 95 % confidence interval of coefficients in bold excluded 0.

Parameters	Soil moisture (FDis)		Light (FDis)		Nutrient (FDis)	
	Estimate (±SE)	(95 % CI)	Estimate (±SE)	(95 % CI)	Estimate (±SE)	(95 % CI)
Longitude	0.011 (±0.011)	(-0.010; 0.033)	0.047 (±0.011)	(0.025; 0.068)	-0.080 (±0.011)	(-0.101; -0.059)
Date	-0.058 (±0.020)	(-0.097; -0.019)	0.061 (±0.020)	(0.021; 0.100)	-0.024 (±0.019)	(-0.061; 0.013)
Elevation	-0.052 (±0.014)	(-0.079; -0.025)	0.004 (±0.014)	(-0.024; 0.031)	0.048 (±0.013)	(0.022; 0.074)
Distance	0.007 (±0.013)	(-0.019; 0.033)	0.008 (±0.016)	(-0.023; 0.039)	0.054 (±0.016)	(0.023; 0.084)
Thickness	-0.009 (±0.014)	(-0.037; 0.019)	0.055 (±0.012)	(0.030; 0.079)	-0.060 (±0.014)	(-0.088; -0.032)
Texture	0.005 (±0.014)	(-0.022; 0.033)	-0.026 (±0.013)	(-0.052; 0.000)	0.061 (±0.014)	(0.033; 0.089)
Date*Elevation	-0.022 (±0.020)	(-0.061; 0.017)	-0.018 (±0.021)	(-0.060; 0.023)	-0.022 (±0.019)	(-0.059; 0.016)
Date*Distance	-0.005 (±0.021)	(-0.046; 0.036)	-0.028 (±0.021)	(-0.070; 0.013)	-0.058 (±0.019)	(-0.097; -0.020)
Date*Thickness	-0.022 (±0.021)	(-0.063; 0.019)	-0.007 (±0.020)	(-0.046; 0.033)	0.027 (±0.019)	(-0.010; 0.064)
Date*Texture	-0.018 (±0.021)	(-0.059; 0.023)	-0.009 (±0.021)	(-0.050; 0.032)	-0.027 (±0.019)	(-0.064; 0.010)
Parameters	Competitive (FDis)		Stress-tolerant (FDis)		Ruderal (FDis)	
	Estimate (±SE)	(95 % CI)	Estimate (±SE)	(95 % CI)	Estimate (±SE)	(95 % CI)
Longitude	-0.057 (±0.010)	(-0.077; -0.037)	-0.031 (±0.010)	(-0.051; -0.011)	-0.002 (±0.012)	(-0.025; 0.022)
Date	-0.019 (±0.017)	(-0.052; 0.015)	0.039 (±0.018)	(0.004; 0.073)	0.077 (±0.021)	(0.035; 0.119)
Elevation	0.020 (±0.012)	(-0.003; 0.043)	0.030 (±0.012)	(0.007; 0.053)	0.050 (±0.013)	(0.024; 0.076)
Distance	-0.008 (±0.011)	(-0.030; 0.013)	0.015 (±0.013)	(-0.011; 0.040)	0.063 (±0.018)	(0.027; 0.098)
Thickness	-0.025 (±0.011)	(-0.046; -0.004)	-0.006 (±0.014)	(-0.033; 0.021)	-0.008 (±0.014)	(-0.036; 0.019)
Texture	0.016 (±0.011)	(-0.005; 0.037)	0.022 (±0.014)	(-0.006; 0.050)	0.034 (±0.014)	(0.007; 0.062)
Date*Elevation	-0.017 (±0.017)	(-0.051; 0.017)	-0.016 (±0.018)	(-0.051; 0.018)	-0.009 (±0.021)	(-0.051; 0.033)
Date*Distance	0.000 (±0.017)	(-0.034; 0.034)	-0.022 (±0.018)	(-0.057; 0.013)	-0.055 (±0.022)	(-0.097; -0.013)
Date*Thickness	0.008 (±0.017)	(-0.026; 0.041)	0.029 (±0.018)	(-0.006; 0.064)	0.015 (±0.022)	(-0.028; 0.059)
Date*Texture	-0.002 (±0.017)	(-0.035; 0.032)	-0.030 (±0.018)	(-0.065; 0.005)	-0.014 (±0.022)	(-0.057; 0.029)

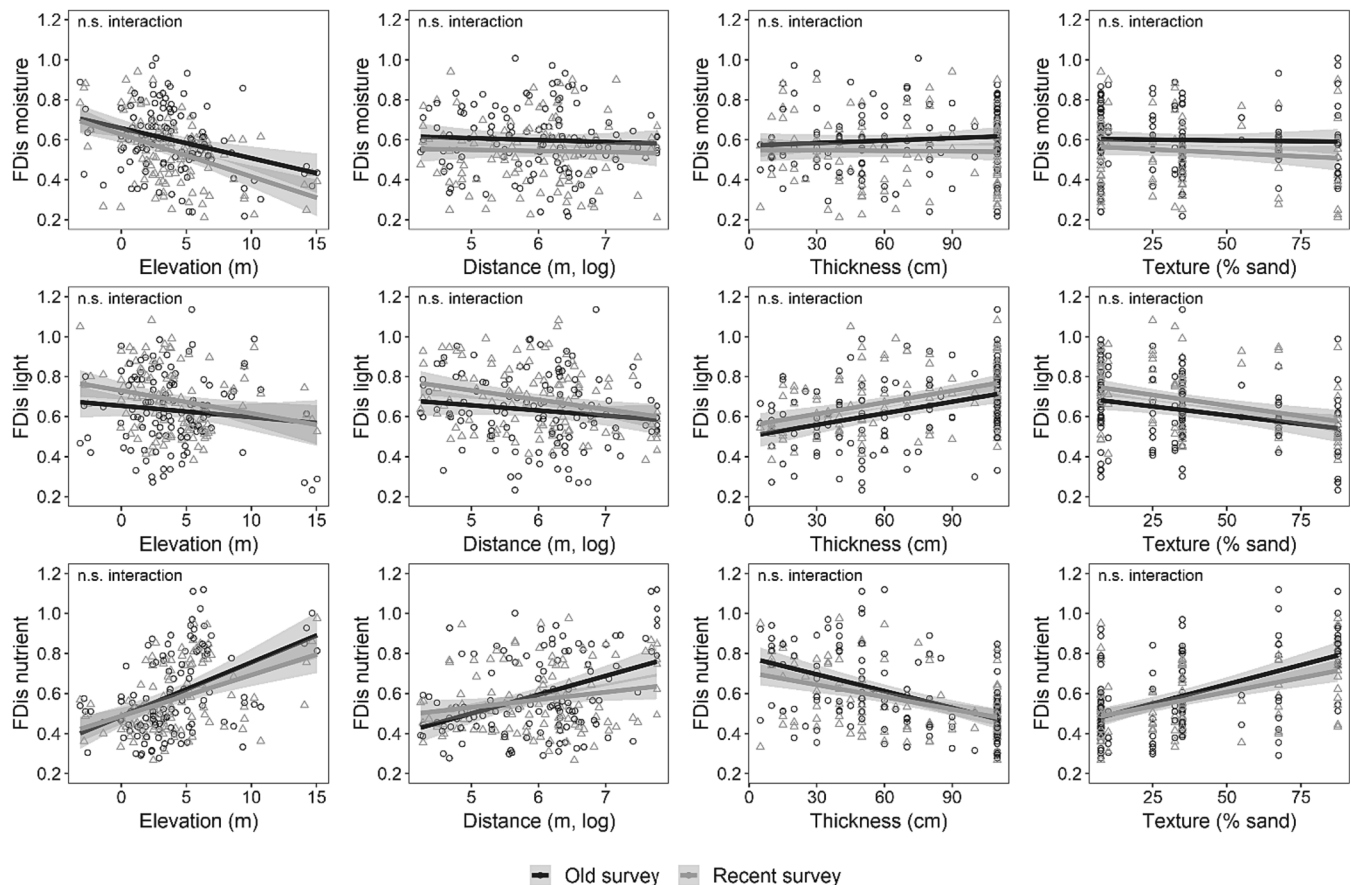


Fig. 4. Variation in the dispersion (FDIs) values of ecological preferences (Ellenberg' values) of riparian communities with connectivity and soil variables between the old and recent surveys, along the Upper Rhône and Ain rivers, France (n.s. interaction = non-significant environmental variable \times Date interaction).

drought stress and shorter flood durations (Díaz-Alba et al., 2023) and therefore to human impact on the hydrology of rivers (González et al., 2018). Complementarily, our results revealed that the mean value for light decreased while the dispersion value for light, i.e., the co-occurrence of heliophilous and sciaphilous species within communities, increased between old and recent surveys. These changes indicated that current communities were composed of more sciaphilous species and that these species were in addition to the heliophilous species still well represented in the communities. This change can be illustrated by the significant increase in the presence of understory species, e.g., *Hedera helix*, *Brachypodium sylvaticum* and *Rubus fruticosus*, in recent surveys. Coupled with the numerous post-pioneer woody species that characterise recent surveys, e.g., *Crataegus monogyna*, *Cornus sanguinea*, *Fraxinus excelsior*, *Prunus mahaleb* and *Acer campestre*, these results show that ecological successions have occurred within communities and that many survey points have evolved towards a more closed and less hygrophilic wooded stage.

Regarding variation in ecological preferences of riparian plant communities along environmental gradients, only one interaction with time spent between the two surveys was significant. Thus, our results showed that the dispersion values for nutrients, i.e., the co-occurrence of oligotrophilous and eutrophilous species within communities, increased less with distance from the riverbed in recent than in old vegetation surveys. This indicates that the current less connected riparian communities were composed of species with more similar nutrient requirements and suggested a homogenization of the productivity gradient over time. Nevertheless, mean and dispersion values of other species ecological preferences responded consistently to environmental gradients. This suggests that changes in environmental conditions between the two dates, as approximated by Ellenberg indicator values,

were homogeneous along the connectivity or productivity gradients studied. It was thus shown that an increase in elevation relative to the riverbed induced a decrease in mean and dispersion values of soil moisture, i.e., that the co-occurrence of hygrophilous and xerophilous species within communities at low elevation converged toward xerophilous species at high elevation for both old and recent surveys, but the representativeness of hygrophilous species decreased overall with time at both ends of the gradient. These results are consistent with those of Mikulová et al. (2020) who also found a decrease in hygrophilous communities over time in relation to changes in water regime. Similarly, for the productivity gradient, it was shown that an increase in silt thickness induced a decrease in mean light values but an increase in dispersion values, and conversely for the proportion of sand in soil. This indicates that, in both old and recent surveys, the co-occurrence of sciaphilous and heliophilous species within communities was stronger on plots with high silt accumulations and converged toward heliophilous species for communities established on gravel or sand bars, but that overall, the representativeness of sciaphilous species increased over time, regardless of soil properties. These results confirm that riparian communities have evolved into more closed mature forest habitats, even more rapidly on fertile banks where biomass productivity is higher (Janssen et al., 2020). These overall changes in environmental conditions can be explained by the decrease in overbank flows and bedload transport (Vázquez-Tarrio et al., 2019), as well as the lowering of the water table (Olivier et al., 2009), related to hydroelectric development in the second half of the 20th century. These hydro-morphological changes in turn reduced the wet and periodically rejuvenated surfaces, allowing ecological succession to take place and therefore the progressive closure of the riparian environment through the establishment of a permanent forest cover dominated by post-pioneer species (e.g.,

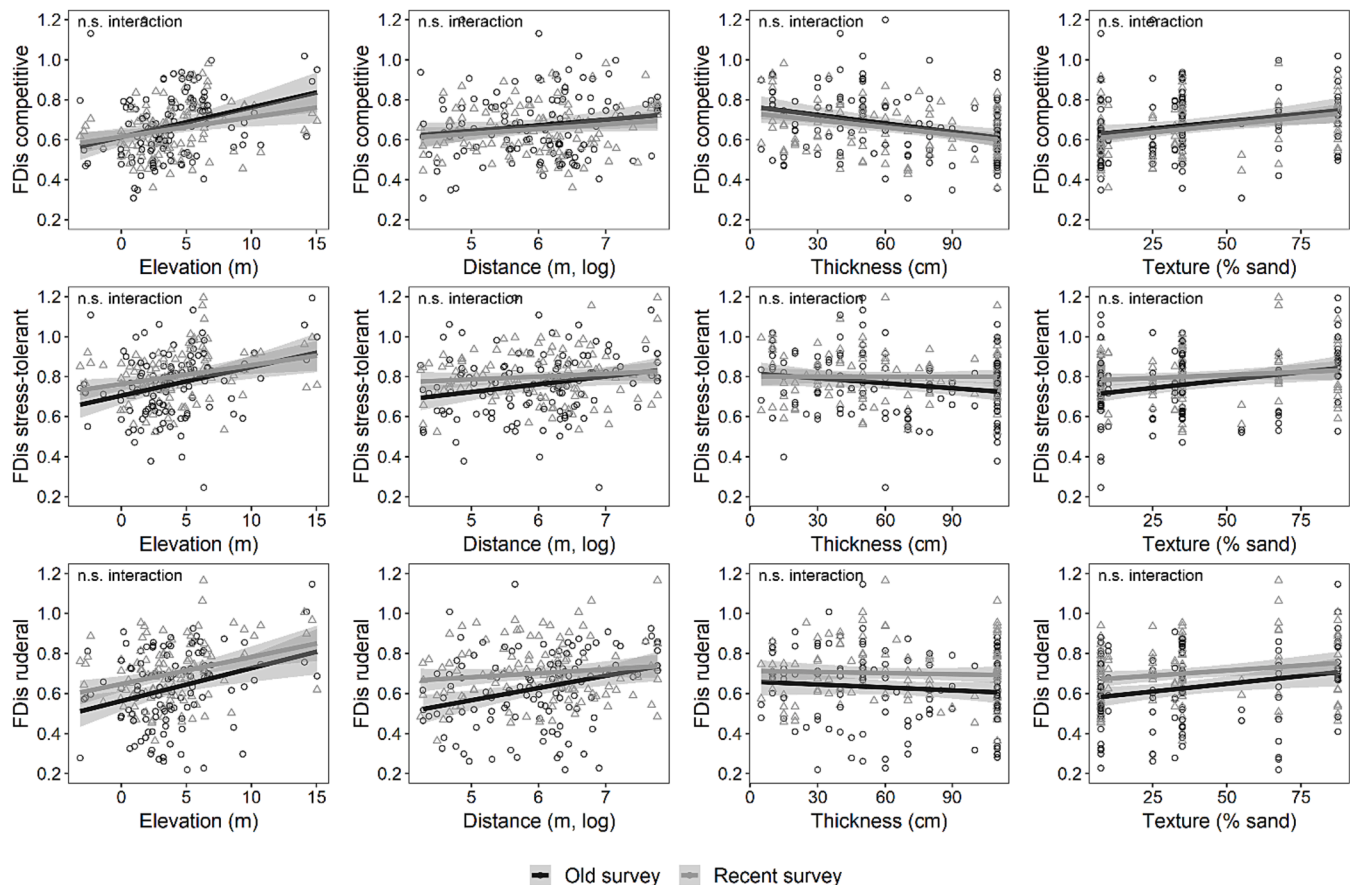


Fig. 5. Variation in the dispersion (FDIs) values of ecological strategies (Grime' values) of riparian communities with connectivity and soil variables between the old and recent surveys, along the Upper Rhône and Ain rivers, France (n.s. interaction = non-significant environmental variable \times Date interaction).

Garófano-Gómez et al., 2013; Marston et al., 1995; Olivier et al., 2009).

4.2. Riparian communities have evolved into more competitive and less stress-tolerant strategies

In response to environmental changes over the past 40 years, the ecological strategies of riparian communities have evolved. Thus, the mean value for competitors has increased while the mean value for stress-tolerators has decreased between old and recent surveys. Consistent with changes in the ecological strategies of species along successional trajectories (Grime, 1977), these results confirm that most of the plots surveys have evolved into more stable and productive environments, i.e., in the case of riparian forests into post-pioneer stages, where biotic interactions gradually replace environmental selection processes (Chen, 2023; Han et al., 2021). In addition, these results highlighted that the stress gradient was reduced, probably due to the regulation and stabilization of flows in bypassed channels, thus limiting the effects of summer low flows (Baxter, 1977), but also due to the development of a denser forest canopy, thus tempering variations in air temperature and relative humidity in the understory (Barbier et al., 2008). Furthermore, we found that the dispersion values for stress-tolerators and ruderals have increased with time, meaning that current communities exhibited a larger range of R- and S-values. This indicates that the co-occurrence of stress-tolerant and ruderal species increased, due to the addition of species with low S-values (e.g., *Clematis vitalba*, *Dioscorea communis*, *Galium aparine*) in the former case, which also induced a decrease in the mean value, and the addition of species with both low (e.g., *Crataegus monogyna*) and high (e.g., *Hedera helix*) R-values in the latter case. This pattern confirms that riparian habitats along the Upper Rhône have become less stressful over time, allowing species better adapted to the

new conditions, i.e., with low S-values, to become established in old vegetation plots. This also shows that species that have increased in presence in current communities, mostly understory herbs and post-pioneer woody species, have a greater range of R-values, even though none of them were strictly ruderal (i.e., the most ruderal species was *Hedera helix* with an R-value of 50.93).

The response of riparian plant communities to environmental gradients allowed us to better understand the previously mentioned changes in ecological strategies over time. Thus, the significant interaction between the distance to riverbed and survey date for the mean value of stress-tolerators and ruderals revealed that communities established close to the riverbed were, on average, more stress-tolerant but less ruderals in older surveys than in recent ones. Considering the theoretical insights from the CSR framework (Grime, 1977), these results may suggest that riparian habitats close to the water level are nowadays less stressful but more disturbed than 40 years ago. Interestingly, however, the interaction between distance to riverbed and survey date was also significant for the dispersion values of ruderals, with greater co-occurrence of species with different R-values near the riverbed in current communities. Taken together, these results revealed that riparian communities on gravel bars and transitional zones were enriched with species with higher R-values, in addition to the species that characterized the old vegetation plots. Further graphical analyses showed a strong spatial effect, confining this interaction effect to the western part of the study area (Appendix S6). As the lower Ain Valley and the Miribel-Jonage area are included in Natura 2000 sites where land clearing by eco-pasture has been carried out for several decades to limit the development of woody plants, it is hypothesized that this enrichment in species with a higher R-value reflects in part the ecological response of communities to grazing disturbance (Green and Kauffman, 1995; Rysiak

et al., 2021). Finally, with regard to the increase in competitors between the two dates, a consistent response was found for connectivity and productivity gradients. Thus, it was shown that increasing elevation and distance from the riverbed, as well as the proportion of sand in soil, induced a decrease in mean C-values, while increasing silt thickness induced an increase in mean C-values, for both old and recent surveys. This confirms that competitive communities become dominant in resource-rich, low-stress environments, i.e., where environmental selection processes are most reduced (Grime, 1977). This pattern is well illustrated by the numerous post-pioneer woody species with a dominant competitive dimension, e.g., *Acer campestre*, *Fraxinus excelsior*, *Viburnum lantana*, which now dominate the plant communities on the studied banks, especially Bregnier-Cordon reach (Pautou et al., 1992). Oppositely, in riparian habitats dominated by coarse sediments, xeric conditions have favored the development of dry grasslands and shrubby thickets sheltering species with high S-values, as previously described in the lower Ain valley (Marston et al., 1995).

5. Conclusion

On the Upper Rhone, Bravard et al. (1986) predicted that the construction of the hydroelectric power station would result in the disappearance of functional units whose survival depended on alluvial processes (*Salix alba*), but the development of units representing the last stages of succession (*Fraxinus excelsior*). By repositioning and resurveying numerous historical plots located partly in the same reach of the upper Rhone, we demonstrated the validity of these predictions. Specifically, we showed that the riparian environment, as approximated by Ellenberg values, shifted toward less hygrophilic and more sciaphilic conditions and that in response, the ecological strategies of communities, as assessed by Grime's CSR values, shifted toward more competitive and less stress-tolerant strategies. These long-term changes in ecological preferences and ecological strategies of riparian communities reveal that, on this regulated and channelized reach of about 100 km, the river dynamics were not strong enough to induce a rejuvenation of all or part of the riparian habitats and thus reinitialize successions. It can therefore be inferred that the shifts observed towards more stable environmental conditions and more mature, closed successional stages express the legacy effects of mid-20th century civil engineering works, which had a major impact on the frequency and magnitude of hydrogeomorphological processes (Vázquez-Tarrío et al., 2019). These findings reveal the long-term impacts that anthropogenic developments have on rivers and related riparian vegetation, inducing a directional shift in riparian communities toward more competitive and less stress-tolerant post-pioneer species (see also, Staude et al., 2022). In a context where past and present anthropogenic stressors are accumulating, with strong effects on aquatic and terrestrial communities (Janssen et al., 2020; Smeti et al., 2019; Stella and Bendix, 2018), it is foreseeable that these changes in riparian ecosystem properties are probably irreversible and represent a major challenge for restoration. Indeed, in addition to the direct alteration of the disturbance regime due to damming, the gradual disappearance of stress-tolerant pioneer species, illustrated here by the temporal decline of the white willow, should promote biotic homogenization of communities at the reach scale (Olden and Rooney, 2006) and, ultimately, greater vulnerability of the system due to the removal of this key functional group of species (Folke et al., 2004).

Authors contribution

V.B. conceived and designed the experiments. V.B. and J.G. collected the data. V.B. and P.J. analysed the data and wrote the first draft of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data can be accessed through the Recherche Data Gouv multidisciplinary repository: <https://doi.org/10.57745/B2OYXV>.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2023.111015>.

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