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The accumulation of anthropogenic stressors induces a progressive shift in the ecological preferences and morphological traits shared by riparian plant communities

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Abstract

1. In riverine ecosystems, human-induced stressors related to flow regulation and bank stabilization have accumulated over time. The restoration of these highly anthropized ecosystems has become a major issue over the last few decades, with ambitious stated objectives. However, while the individual impact of flow regulation and channelization on river functioning has been extensively studied, the response of ecological communities to multiple co-occurring human-induced stressors remains largely unexplored.

2. Using a sampling design based on five river reaches in the Rhône catchment, ranging from unregulated in flow and bedload transport to intensively regulated reaches, we sought to understand how the accumulation of anthropogenic stressors influenced the functional response of riparian plants communities on gravel bars. By using twelve ecological and morphological traits, we performed a classification analysis to construct six riparian guilds and investigated whether their representativeness, as well as the mean value of individual traits, varied with increasing levels of anthropogenic stressors.

3. Species cover and redundancy in several guilds increased or decreased significantly with increasing pressures. Thus, the guild of small taproot herbs with low nutrient and soil moisture requirements (xero-oligotro-taproot species guild) and the guild of taproot herbs adapted to very bright and dry conditions (mesoxero-mesotro-taproot species guild) dominated the unregulated reaches with active bedload transport. Conversely, regulated reaches with stabilized baseflow and inactive transport were dominated by the guild of flood-tolerant trees (hygro-perennial tall species guild) and the guild of vegetatively reproducing and flood-tolerant perennial herbs (hygro-perennial clonal species guild).

4. Analysis of individual traits revealed a shift in environmental conditions, from full light to shade tolerance and from dry to humid, with increasing anthropogenic stressors. In response to this decrease in drought levels, plants traits shifted from annual to perennial species, from sexual to vegetative strategies and from taproots to a fibrous root system.

5. Our results highlight the accumulated effects that anthropogenic stressors can have on riparian communities, inducing a progressive shift in certain traits related to life history, reproductive strategies and drought adaptations. This effect on a set of shared traits reveals the strong influence that human infrastructures can have on the ecological niche of species and the morphological adaptations of riparian vegetation.

6. From an applied point of view, and for highly anthropized rivers, our results suggest that restoration actions targeting a single stressor will not be sufficient to reorient riparian plant communities towards an ecological state closer to reference systems. Since human-induced stressors have often deeply altered the flow and sediment regimes of rivers, a more integrated approach based on the restoration of erosion and flooding processes is essential to allow the expression of a wider diversity of riparian plant communities and habitats.

Keywords: bank channelization, flow regulation, guild, gravel bar, traits based-approach

1. Introduction

Riverine ecosystems and their adjacent riparian zones are among the most threatened ecosystems by anthropogenic stressors (Best, 2019). Throughout the world, rivers have been largely damned and regulated to meet human needs for water and energy or to protect goods and services from flooding (Nilsson *et al.*, 2005). For example, in Europe, Belletti *et al.* (2020) showed that more than one million barriers, such as dams, weirs and fords, fragmented the longitudinal connectivity of rivers. In addition, kilometers of dikes and riprap protections have been built for centuries to stabilize the river banks, preventing lateral erosion processes and limiting the remobilization of coarse sediments (Florsheim, Mount & Chin, 2008). The cumulative impacts of river regulation and stabilization structures have been shown to profoundly disrupt the hydro-geomorphic processes necessary for the proper functioning of lotic environments (Poff *et al.*, 2007; Tena *et al.*, 2020), with detrimental consequences for aquatic and riparian biodiversity (Reid *et al.*, 2019).

In recent decades, the ecological restoration of degraded ecosystems has taken on considerable importance, with ambitious international objectives (e.g., Aichi Biodiversity Targets set by the Convention on Biological Diversity). The European Union's biodiversity strategy has thus set a target of restoring at least 25,000 kilometers of free-flowing rivers by 2030, by removing obsolete dams and restoring riparian habitats (EU Bringing Nature Back Into Our Lives). However, due to possible interaction or hierarchical effects of flow regulation by dams and bank stabilization by dikes, it is not clear that the removal of these engineering structures will restore the ecological quality of the most degraded river ecosystems and reorient the altered communities to their historical trajectories or to more dynamic stages (Reid *et al.*, 2019). To define achievable restoration objectives but also to target the river reaches with the higher potential for improvement, it appears thus fundamental to better understand how ecological communities respond to multiple co-occurring human-induced stressors.

Among the diversity of organisms living in river and riparian areas, terrestrial biota, i.e., vegetation and beetles, have recently been shown to respond more strongly than aquatic biota to hydromorphological restoration operations (Pilotto *et al.*, 2019). Indeed, in addition to playing a critical role in sustaining the structure and functions of rivers, e.g., through regulating and maintenance services (Riis *et al.*, 2020), riparian vegetation can provide a valuable assistance in diagnosing problems, e.g., by linking changes in vegetation to environmental changes (González del Tánago *et al.*, 2021). To date, studies have demonstrated the negative effects of flow regulation, i.e., stabilizing the water line and mitigating the frequency and intensity of floods, on riparian plant communities by homogenizing and simplifying the species pool (Su *et al.*, 2020; Zheng *et al.*, 2021; Friedman *et al.*, 2022). Also, bank stabilisation, by limiting sediment remobilization and promoting channel incision, induced a decrease in species richness and a change in composition in favor of drought-tolerant species (Baatrup-Pedersen *et al.*, 2005; Helfield *et al.*, 2007; Dufour *et al.*, 2007). However, and despite the fact that many large rivers have been both damned and channelized (e.g., Alexander, Wilson & Green, 2012; Arnaud *et al.*, 2015; Luan *et al.*, 2018), very few studies have investigated the cumulative impact of altered water flow and sediment transport on riparian plant communities.

Here, we sought to understand how several anthropogenic stressors influenced the functional response of riparian plant communities on gravel bars. Composed of accumulations of alluvial sediments, gravel bars are

dynamic and morphologically complex riparian habitats that support rich communities, including threatened plant and animal species (e.g., Zeng *et al.*, 2015; Rottenborn, Vítovcová & Prach, 2018). We selected five river reaches in the Rhône catchment, ranging from a near-natural reference reach to a highly anthropized and intensively managed reach, and studied the response of gravel bar plant communities to changes in flow regulation and bedload transport. Because the five river reaches were geographically distant, with partially different local species pools, but also because we wanted to understand in a more mechanistic way the response of plant communities to anthropogenic stressors, we mobilized a trait-based approach. Unlike taxonomy-related measures, species traits allow for the study of various aspects related to resource use, dispersal strategies, or competitive interactions and are therefore useful measures for understanding the links between environmental changes, assemblage structures, and processes in ecosystems (Lavorel *et al.*, 2008). Numerous studies have provided a detailed understanding of the mechanisms that shape riparian plant communities, either by studying variations in the mean value of individual traits (e.g., Kyle & Leishman, 2009; Lawson, Fryirs & Leishman, 2015; McCoy-Sulentic *et al.*, 2017) or by using the information contained in quantitative and qualitative traits to construct guilds (e.g., Stromberg & Merritt, 2016; Bejarano, Nilsson & Aguiar, 2018; Bejarano *et al.*, 2018). However, most of these studies have focused on tree species in alluvial forests (e.g., Bejarano *et al.*, 2012; Aguiar *et al.*, 2013; Hough-Snee *et al.*, 2015; Cubley *et al.*, 2020; Lozanovska *et al.*, 2020), despite the recognition that herbaceous species respond more rapidly to environmental changes (Stromberg & Merritt, 2016). The original contribution of our work relies thus on three points: (1) the study of the cumulative effect of several anthropogenic stressors; (2) the consideration of herbaceous species in the analysis of community response to these stressors; (3) the comparison of results obtained between the study of variations in the cover and redundancy of species within guilds and the study of variations in the mean values of individual constituent traits of guilds.

Specifically, we hypothesised that changes in the flow regime, due to the attenuation of the flood peak by dams but also, for some reaches, the stabilization of baseflow, will induce a functional response of riparian plant communities that will favor (1) drought adaptative traits (e.g., plants with deep taproots adapted to groundwater variability and with low specific leaf areas to conserve acquired resources) and ruderal strategies in unregulated reaches and (2) soil moisture adaptative traits (e.g., plants with fibrous roots adapted to relatively stable groundwater and with high specific leaf areas to intercept and exploit resources) and competitive strategies in regulated reaches. In addition, we hypothesised that changes in bedload transport, due to the interruption of coarse sediment supply upstream but also, for some reaches, the cessation of lateral bar mobility, will induce a functional response of riparian plant communities that will favor (1) disturbance-adaptative traits (e.g., small plants adapted to rapid colonization and with sexual reproduction to feed the soil seed bank) and annual life forms in reaches with active transport and (2) stable-environment-adaptative traits (e.g., tall plants adapted to compete for light and with vegetative reproduction to spread rapidly and dominate the environment) and perennial life forms in reaches with inactive transport. Finally, we hypothesised that changes in flow regimes and bedload transport will have cumulative effects on the functional response of riparian plant communities that will promote (1) a progressive shift of a set of traits related to the ecological preferences, the ecological strategies and the morphology of the species and (2) a strong environmental

filtering that will clearly separate communities in unregulated reaches with active transport from those in regulated reaches with inactive transport.

2. Material and Methods

2.1. Location and experimental design

The study was carried out along the Rhône River (total length = 810 km, catchment area = 96,500 km², mean annual discharge = 1,700 m³ s⁻¹) and two tributaries: the Drôme River (total length = 110 km, catchment area = 1,663 km², mean annual discharge = 20 m³ s⁻¹) and the Ain River (total length = 190 km, catchment area = 3,765 km², mean annual discharge = 123 m³ s⁻¹) (Figure 1). These rivers are located in SE France and experience a temperate climate with mean annual temperature and precipitation of 13.6 °C and 755 mm in the southern part and of 11.9 °C and 782 mm in the northern part. Despite differences in catchment size and discharge magnitude, the rivers prior to human modification shared similar snowmelt flow regimes and sediment dynamics.

The Drôme River is a free-flowing river with a shifting braided pattern over a significant length of its downstream section. The Ain River is regulated by a series of five dams in its upstream section, built in the 20th century (between 1933 and 1968), which triggered a shift from a braided to a free meandering channel in its downstream section (Marston *et al.*, 1995). These two piedmont rivers are mostly unconstrained by human infrastructure and still have a significant bedload transport but have experienced channel narrowing since the second half of the 20th century due to long-term bedload supply decrease (Liébault & Piégay, 2002). Both river reaches are still subject to periodic floods that allow active bedload transport, flooding, channel shifting and associated renewal of riparian vegetation (see Figures S1, S2 & S3). The middle reach of the Rhône River is a highly modified section, which has shifted from a braided pattern to a series of impounded reaches within the span of approximately one century. Two historical management phases have greatly modified the river: a correction phase during the 19th century, characterized by the construction of an extensive system of longitudinal submersible and transversal dikes in the main channel to facilitate navigation, followed by a derivation phase in the second half of the 20th century, characterized by the construction of a series of lateral canals, parallel to the river's natural channel, in order to generate hydropower and facilitate irrigation and navigation (for details see, Bravard and Gaydou 2015). These two development phases induced significant impacts in the bypassed reaches, including a channel dewatering due to flow by-passing, reduction in the frequency and magnitude of the peak flows (Vázquez-Tarrío *et al.*, 2019), and channel incision and lateral stabilization (see Figures S1, S2 & S3). Thus, with the exception of the Miribel-Jonage bypassed reach, these reaches also underwent a bedload supply interruption at the tributary confluences inducing gravel winnowing and bed armouring within the main branch. Their present-day bedload transport is limited to fine-grained sediments (Vázquez-Tarrío *et al.*, 2019). To prevent channel narrowing due to encroachment of woody vegetation, most riparian habitats in the riverbed of bypassed reaches are maintained by either brush clearing or plowing.

Two gravel bars were sampled during the summers of 2017 and 2018 on each of the five river reaches (n = 10, Figure 1): unregulated reach with active bedload transport (Drôme River, DRM, n = 2); regulated reach with active bedload transport (Ain River, AIN, n = 2); regulated reach with stabilized baseflow and active bedload transport (Rhône River, Miribel-Jonage bypassed reach, MRJ, n = 2); regulated reach with stabilized baseflow and inactive bedload transport, with riparian vegetation management by brush clearing (Rhône River, Pierre-Bénite bypassed reach, PBN, n = 2) or plowing (Rhône River, Donzère-Mondragon bypassed reach, DZM, n = 2). These five reaches are ordered to represent an increasing level of anthropogenic stressors (i.e., DRM, AIN, MRJ, PBN, DZM), ranging from near-natural reference rivers to highly anthropized and intensively managed rivers.

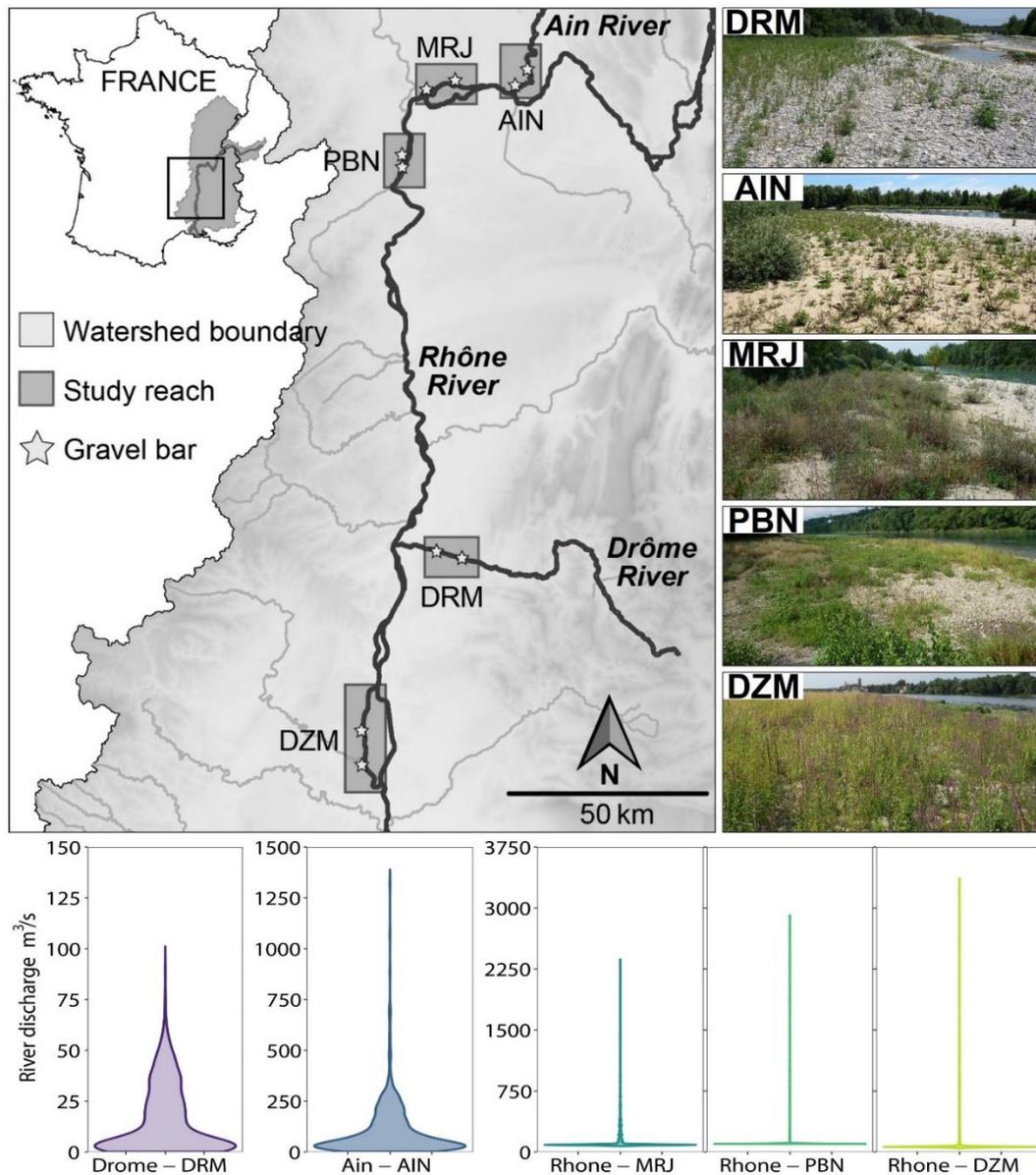


Figure 1. Location of the study area in the Rhône River catchment, distribution of sampled gravel bars within river reaches and violin plots representing the frequency distribution of flows for the five studied reaches. DRM = Drôme River (unregulated + active bedload transport); AIN = Ain River (regulated + active bedload transport); MRJ = Rhône River, Miribel-Jonage bypassed reach (regulated + stabilized baseflow + active bedload transport); PBN = Rhône River, Pierre-Bénite bypassed reach (regulated + stabilized baseflow + inactive bedload transport + managed by brush clearing); DZM = Rhône River, Donzère-Mondragon bypassed reach (regulated + stabilized baseflow + inactive bedload transport + managed by plowing) (see also Figures S1, S2 & S3)

2.2. Vegetation data and trait selection

On each gravel bar, the vegetation was surveyed within twelve 5 x 5 m quadrats (25 m²) positioned along three transects (four quadrats per transect) oriented perpendicularly to the river, in areas with clear elevation gradients relative to the water surface (for details see, Janssen, Piégay & Evette, 2022b). Transects were spaced approximately 100 m apart and located to cover the upstream, middle and downstream portion of the gravel bars. All vascular plants were surveyed following the Braun-Blanquet abundance-dominance methodology. To characterize the entire plant community and account for plant phenology, two complete surveys were conducted each year (June and July), and to limit observer biases, all surveys were performed by the same person (PJ).

For each species present in at least 5% of the quadrats (i.e., $n = 172$ out of a total of 219 species), we collected data on ecological preferences, ecological strategies, morphological traits and life cycle (referred to as "trait" in the manuscript, see also Table S1 & Figure S4). Ellenberg's indicator values (Ellenberg *et al.*, 1992) for light (L), nitrogen content (N) and soil moisture (F) were extracted from the Baseflor database (Julve, 1998) and used to characterize variations in species habitat niche. Grime's values (Grime, 1977) for 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 plants. Westoby's values (Westoby, 1998) for specific leaf area (SLA), plant height and seed mass were extracted from the TRY database (Kattge *et al.*, 2020) and used to characterize variations in resource acquisition, competitive and dispersal abilities. Three qualitative traits were also considered: clonality (yes vs no) and root type (taproot vs others) were extracted from the TRY database while plant life form (annual/biennial vs perennial) was extracted from the Baseflor database.

2.3. Environmental data

At each quadrat center, the elevation difference and distance to the water line was characterized using topographical surveys. Topographic measurements were conducted using a laser rangefinder (TruPulse 200X) positioned on a tripod at a constant height of 1.20 m and a target at a height of 2 m. The horizontal and vertical distances between the tripod and the target were measured between the water at the beginning of each transect and the center of the four successive quadrats. Soil textural properties were derived from two soil core samples collected in representative areas of each quadrat and pooled. Each composite soil sample was then dried, weighed and sieved to estimate the proportion of fine sediments (i.e., <250- μ m mesh). Moreover, fine sediment thickness was estimated at the center of each quadrat using a soil corer inserted into the sediment up to the interface with the gravel and measuring the distance from the surface.

2.4. Data analysis

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

To determine whether the topographic (i.e., elevation difference and distance to water) and soil texture properties (i.e., proportion and thickness of fine sediments) of gravel bars were under relatively similar

environmental conditions between river reaches, we used one-way ANOVAs and Tukey's HSD post hoc tests (car package, Fox & Weisberg, 2019).

To determine whether the representativeness of riparian plant guilds varied between the river reaches, we used a three-step analytical strategy. First, because we were interested in analysing the response of plant communities to increasing levels of anthropogenic stressors at the gravel bar scale, we used the transect as the baseline level of observation ($n = 6$ by reach). Therefore, we pooled all species present in at least one of the four quadrats along each transect and summed up the related cover for each species. Second, to obtain guilds, we replicated the methodology used in riparian ecology (e.g., Hough-Snee *et al.*, 2015; Aguiar *et al.*, 2018; Su *et al.*, 2020) by performing a hierarchical cluster analysis (Ward method) on a Gower distance matrix of species ($n = 172$) by traits ($n = 12$) data. Since the classical Gower distance produce a disproportionate contribution of qualitative traits to the multi-trait dissimilarity, we used the 'gawdis' R function (de Bello *et al.*, 2021). The optimal number of guilds was determined by maximizing the F-value of a PERMANOVA (Anderson & Walsh, 2013) with 999 permutations (vegan package, Oksanen *et al.*, 2013), for a solution fixed between 5 and 8 guilds. Then, to validate the groups obtained based on biological knowledge, we tested for variation in each of the individual traits between guilds using one-way ANOVAs with Tukey's HSD post hoc tests for quantitative traits, and Chi-square with post hoc tests for qualitative traits. To illustrate the different guilds, we also identified the most frequent species in each guild. Third, we tested how species redundancy (i.e., the ratio of the number of species in the transect to the total number of species in the guild) and species cover (i.e., the accumulated cover of related species in each transect) within each guild varied between the reaches using Kruskal-Wallis and Dunn's post hoc tests (p -values adjusted with the Benjamini and Hochberg correction). To determine whether individual trait value varied between river reaches, we used a two-step analytical strategy. First, we computed the community-weighted means (CWM) using species cover determined at the transect scale as a measure of relative abundance (FD package, Laliberté, Legendre & Shipley, 2014). To compare the effect of individual traits on a common scale, they were all normalized to vary between 0 and 1. Also, because seed mass and plant height of a few species were very high, these two traits were log-transformed before CWM calculation. Second, we tested how the normalized mean value of each trait varied between the river reaches using Kruskal-Wallis and Dunn's post hoc tests (p -values adjusted with the Benjamini and Hochberg correction).

3. Results

3.1. Variations in environmental conditions between river reaches

ANOVAs revealed significant variations in topographical and soil texture variables between river reaches (Table 1 & Figure 2). Pairwise comparisons (Table S2) showed that the gravel bars on DRM were at a significantly lower mean topographic level than those on MRJ and PBN and that the gravel bars on DZM were lower than those on MRJ. In addition, the mean proportion of fine sediments was significantly lower on AIN than on PBN and DZM. Finally, the mean thickness of fine sediments was significantly higher on PBN than on DRM and AIN.

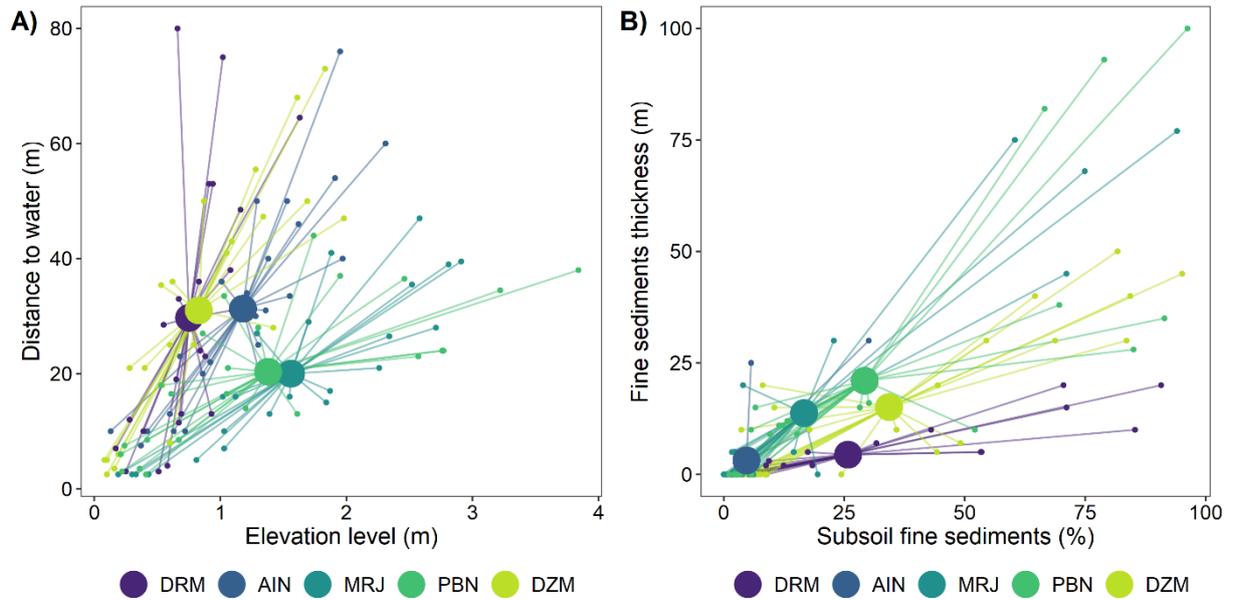


Figure 2. Variations in topographic (A) and soil texture (B) variables, within and between gravel bars, along the five river reaches studied (DRM = Drôme, AIN = Ain, MRJ = Miribel-Jonage, PBN = Pierre-Bénite, DZM = Donzère-Mondragon; small dots indicate measured values at the quadrat scale, colored lines connect each quadrat to the average values for the corresponding river reach, represented by large dots)

Table 1. Variations in environmental conditions between the five river reaches studied (DRM = Drôme, AIN = Ain, MRJ = Miribel-Jonage, PBN = Pierre-Bénite, DZM = Donzère-Mondragon; $F_{(4,115)}$ and p-value based on one-way ANOVA)

Variable	Mean (\pm SD)					F-value	p-value
	DRM	AIN	MRJ	PBN	DZM		
Elevation above water line (m)	0.75 (\pm 0.33)	1.18 (\pm 0.56)	1.56 (\pm 0.83)	1.38 (\pm 1.06)	0.83 (\pm 0.59)	5.604	0.000
Distance to water line (m)	29.71 (\pm 22.59)	31.29 (\pm 18.19)	20.00 (\pm 13.58)	20.33 (\pm 12.52)	31.01 (\pm 20.63)	2.497	0.047
Proportion of fine sediments (%)	25.79 (\pm 29.04)	4.71 (\pm 6.61)	16.67 (\pm 27.79)	29.25 (\pm 33.13)	34.30 (\pm 31.31)	3.625	0.008
Thickness of fine sediment (cm)	4.42 (\pm 6.26)	3.12 (\pm 7.91)	13.75 (\pm 25.57)	21.00 (\pm 29.30)	15.08 (\pm 16.63)	4.380	0.002

3.2. Variations in species cover and redundancy in guilds between river reaches

Based on the classification analysis and the maximisation of the F-value, six riparian guilds were identified. One-way ANOVAs and Chi-square tests revealed that all quantitative and qualitative traits varied significantly between guilds (Table S3). Guild naming was done on the basis of significant differences (Table 2), for each of the trait values, between pairs of guilds (Table S4) and following the recommendations of Lozanovska et al. (2018). The guild of hydro-perennial tall species (G1, n species = 24) gathers most flood-tolerant trees; the guild of hydro-perennial clonal species (G2, n species = 21) gathers most vegetatively reproducing and flood-tolerant perennial herbs; the guild of meso-eutro-annual taproot species (G3, n species = 24) gathers most small annual taproot herbs with high nutrient requirements; the guild of xero-oligotro taproot species (G4, n species = 21)

Table 2. Description of the six riparian guilds of the Rhône, Drôme and Ain gravel bars (France) derived from 172 species and 12 traits (hygrophilous/mesophilous/xerophilous refer to soil moisture, from wet to dry environments; sciaphilous/heliophilous refer to light availability, from shade to full-light environments; oligotrophilous/mesotrophilous/eutrophilous refer to soil nutrients, from poor to fertile environments; see also Tables S3 & S4 for details)

Guild name	Ecological preferences	Ecological strategies	Morphological traits	Life cycle	Species
G1: Hygro-perennial tall species	Hygro-Helio-mesotrophilous	SC	Tall species with large seeds and resource conservation strategies	Perennial	<i>Populus nigra</i> , <i>Phalaris arundinacea</i> , <i>Salix eleagnos</i> , <i>Acer negundo</i>
G2: Hygro-perennial clonal species	Hygro-mesotrophilous	R	Medium-sized clonal species with light seed and resource acquisition strategies	Perennial	<i>Agrostis stolonifera</i> , <i>Lolium perenne</i> , <i>Rorippa sylvestris</i> , <i>Lycopus europaeus</i>
G3: Meso-eutro-annual taproot species	Meso-eutrophilous	R	Small-sized species with taproot and resource acquisition strategies	Annual	<i>Persicaria lapathifolia</i> , <i>Persicaria mitis</i> , <i>Persicaria maculosa</i> , <i>Polygonum aviculare</i>
G4: Xero-oligotro taproot species	Xero-Helio-oligotrophilous	SR	Medium-sized species with taproot and medium-weight seeds	Mixte	<i>Medicago lupulina</i> , <i>Sanguisorba minor</i> , <i>Arenaria serpyllifolia</i> , <i>Poa compressa</i>
G5: Mesoxero-mesotro taproot species	Mesoxero-Helio-mesotrophilous	CSR	Medium-sized species often with taproot and medium-weight seeds	Mixte	<i>Ambrosia artemisiifolia</i> , <i>Melilotus albus</i> , <i>Setaria viridis</i> , <i>Echinochloa crus-galli</i>
G6: Meso-eutro-perennial species	Meso-eutrophilous	C	Medium-sized species often clonal with medium-weight seeds	Perennial	<i>Plantago lanceolata</i> , <i>Elymus repens</i> , <i>Artemisia verlotiorum</i> , <i>Poa trivialis</i>

gathers most small perennial taproot herbs with low nutrient and soil moisture requirements; the guild of mesoxero-mesotro taproot species (G5, n species = 56) gathers most sexually reproducing taproot herbs adapted to very bright and dry conditions; the guild of meso-eutro-perennial species (G6, n species = 26) gathers most vegetatively reproducing and competitive perennial herbs with high nutrient requirements. Kruskal-Wallis tests revealed that, with the exception of the species cover for G3 and the species redundancy for G6, all other measures varied significantly between river reaches (Table 3). Specifically, for G1, G2, G4 and G5, a trend of increasing or decreasing species redundancy and/or species cover with increasing levels of anthropogenic stressors was shown (Figure 3). Dunn's post hoc tests, however, revealed that most pairwise comparisons, after adjustment of p-values by the Benjamini and Hochberg correction, were not significant (Table S5). For G1, species redundancy on DZM (i.e., regulated and stabilized with inactive bedload, managed by plowing) was significantly higher than on DRM (i.e., unregulated with active bedload), AIN (i.e., regulated with active bedload) and MRJ (i.e., regulated and stabilized with active bedload). For G2, species cover on AIN was significantly lower than on MRJ, PBN (i.e., regulated and stabilized with inactive bedload, managed by brush clearing) and DZM and species redundancy on DZM was significantly higher than on DRM and AIN. For G4, species cover and species redundancy on DRM were significantly higher than on MRJ, PBN and DZM. For G5, species cover on DRM was significantly higher than on AIN, MRJ and DZM and species redundancy on DRM was significantly higher than on MRJ, PBN and DZM. For G6, species cover on AIN was significantly lower than on PBN and DZM and species cover on DRM and MRJ were significantly lower than on PBN.

Table 3. Variations in the percentage cover and redundancy of riparian species, for each guild, between the five river reaches studied (DRM = Drôme, AIN = Ain, MRJ = Miribel-Jonage, PBN = Pierre-Bénite, DZM = Donzère-Mondragon; H-stat and p-value based on Kruskal-Wallis test)

Variable	Mean (\pm SD)					H-stat	p-value	
	DRM	AIN	MRJ	PBN	DZM			
Cover (%)	Guild 1	15.75 (\pm 18.39)	15.71 (\pm 11.33)	36.12 (\pm 15.31)	32.92 (\pm 9.25)	33.08 (\pm 9.58)	11.011	0.026
	Guild 2	10.00 (\pm 8.91)	2.38 (\pm 1.21)	16.33 (\pm 7.26)	17.71 (\pm 6.00)	27.92 (\pm 15.87)	15.950	0.003
	Guild 3	8.38 (\pm 7.40)	11.83 (\pm 8.74)	16.12 (\pm 14.17)	4.54 (\pm 0.99)	6.08 (\pm 2.17)	4.297	0.367
	Guild 4	5.50 (\pm 3.54)	3.17 (\pm 2.86)	0.42 (\pm 0.38)	1.29 (\pm 1.73)	0.46 (\pm 0.46)	15.424	0.004
	Guild 5	58.50 (\pm 18.67)	16.79 (\pm 7.31)	13.21 (\pm 8.12)	19.29 (\pm 7.01)	13.75 (\pm 9.49)	13.977	0.007
	Guild 6	13.08 (\pm 5.90)	4.88 (\pm 1.72)	11.50 (\pm 10.28)	42.54 (\pm 4.79)	16.88 (\pm 8.62)	21.005	0.000
Redundancy (%)	Guild 1	29.86 (\pm 9.29)	20.14 (\pm 4.10)	29.86 (\pm 4.87)	31.94 (\pm 4.30)	46.53 (\pm 6.13)	20.456	0.000
	Guild 2	15.87 (\pm 4.92)	15.87 (\pm 9.36)	27.78 (\pm 8.74)	31.75 (\pm 7.17)	47.62 (\pm 9.52)	20.975	0.000
	Guild 3	28.47 (\pm 8.90)	45.83 (\pm 5.27)	43.06 (\pm 12.27)	27.78 (\pm 7.76)	26.39 (\pm 13.61)	12.603	0.013
	Guild 4	37.30 (\pm 8.20)	26.98 (\pm 16.40)	7.14 (\pm 6.56)	7.94 (\pm 7.17)	5.56 (\pm 4.68)	17.512	0.002
	Guild 5	47.32 (\pm 5.73)	31.85 (\pm 4.71)	27.08 (\pm 5.69)	26.49 (\pm 6.72)	19.94 (\pm 7.78)	18.665	0.001
	Guild 6	30.77 (\pm 10.32)	32.69 (\pm 7.20)	40.38 (\pm 10.25)	46.79 (\pm 14.88)	39.10 (\pm 9.55)	6.623	0.157

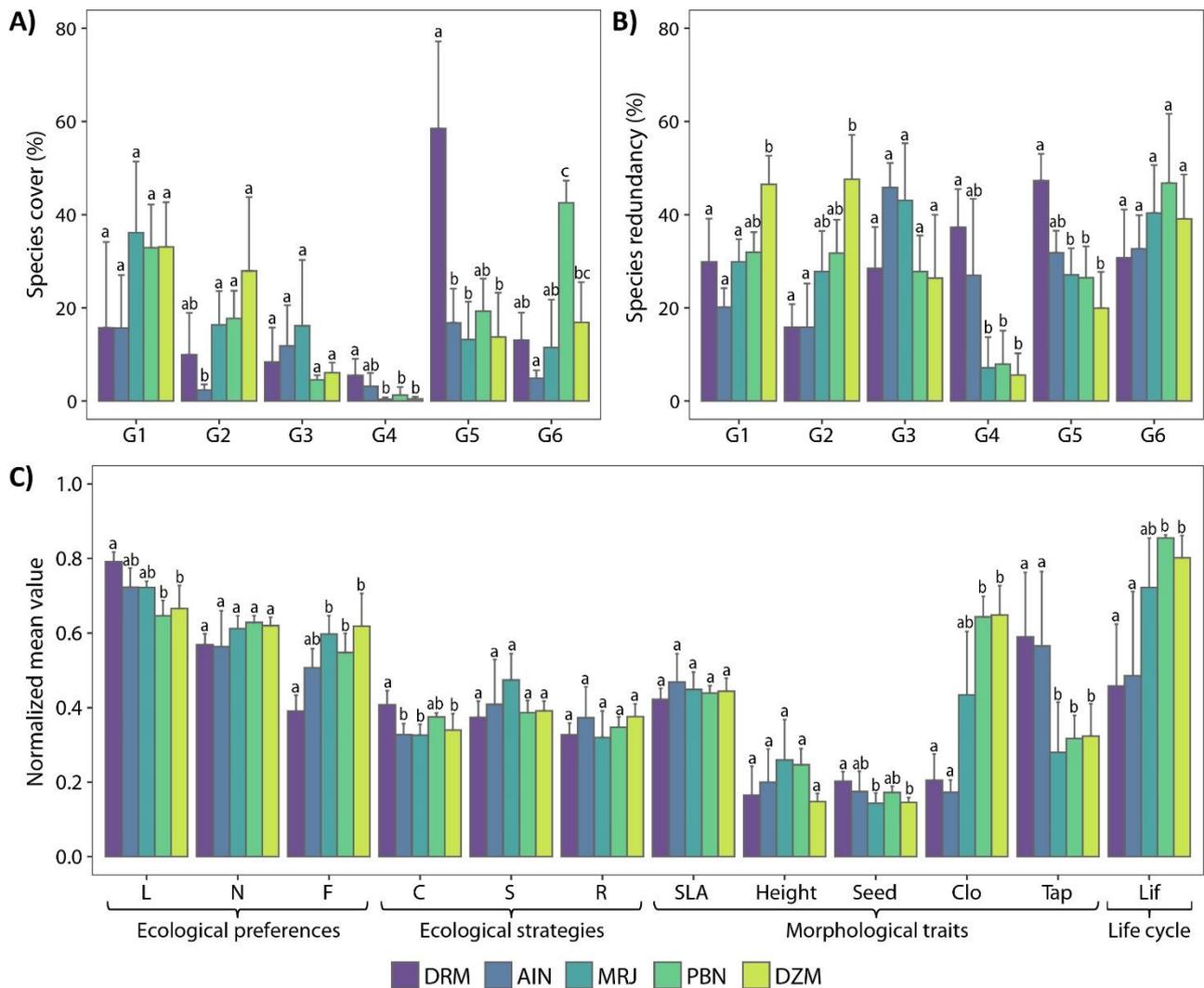


Figure 3. Variations in the percentage cover (A) and redundancy (B) of riparian species for each guild (G1-G6, Table 2), as well as the normalized mean value of individual traits (C) between the five river reaches studied (DRM = Drôme, AIN = Ain, MRJ = Miribel-Jonage, PBN = Pierre-Bénite, DZM = Donzère-Mondragon; L = light requirement, N = nitrogen requirement, F = soil moisture requirement, C = competitive strategy, S = stress-tolerator strategy, R = ruderal strategy, SLA = Specific Leaf Area, Height = plant height, Seed = seed mass, Clo = clonality (yes), Tap = taproot (yes), Lif = life cycle (perennial); bars with different letters indicate significant differences ($p < 0.05$) among factor levels, based on Dunn's post hoc tests, see also Tables 3, 4 & Tables S5, S6)

3.3. Variations in the mean values of individual traits between river reaches

Kruskal-Wallis tests revealed that mean values for light (L) and soil moisture (F) requirements, competitive strategies (C), plant height, seed mass, clonality, taproot and perennial life cycle varied significantly between river reaches (Table 4). As with guilds, a trend of increasing or decreasing mean values with increasing levels of anthropogenic stressors was shown for some of these traits (Figure 3). Dunn's post hoc tests, however, revealed that pairwise comparisons, after adjustment of p-values by the Benjamini and Hochberg correction, were not significant for plant height and limited to a few comparisons for the others traits (Table S6). For ecological preferences, light requirements were significantly higher on DRM (i.e., unregulated with active bedload) than on PBN (i.e., regulated and stabilized with inactive bedload, managed by brush clearing) and DZM (i.e., regulated and stabilized with inactive bedload, managed by plowing), while soil moisture requirements were significantly lower on DRM than on MRJ (i.e., regulated and stabilized with active bedload), PBN and DZM. For ecological strategies, competitors were significantly higher on DRM than on AIN (i.e., regulated with active bedload), MRJ and DZM. For morphological traits, the seed mass was significantly higher on DRM than on MRJ and DZM, the percentage of clonal species was significantly higher on PBN and DZM than on DRM and AIN while the percentage of taproot species was significantly higher on DRM and AIN than on MRJ, PBN and DZM. Finally, for life cycle, the percentage of perennial species was significantly higher on PBN and DZM than on DRM and AIN.

Table 4. Variations in the normalized mean value (i.e., community-weighted means) of each trait between the five river reaches studied (DRM = Drôme, AIN = Ain, MRJ = Miribel-Jonage, PBN = Pierre-Bénite, DZM = Donzère-Mondragon; H-stat and p-value based on Kruskal-Wallis test)

	Variable	Mean (\pm SD)					H-stat	p-value
		DRM	AIN	MRJ	PBN	DZM		
Normalized mean value	Light	0.79 (\pm 0.03)	0.72 (\pm 0.05)	0.72 (\pm 0.02)	0.65 (\pm 0.04)	0.67 (\pm 0.06)	20.576	0.000
	Nitrogen	0.57 (\pm 0.03)	0.56 (\pm 0.10)	0.61 (\pm 0.03)	0.63 (\pm 0.02)	0.62 (\pm 0.02)	6.314	0.177
	Soil moisture	0.39 (\pm 0.04)	0.51 (\pm 0.05)	0.60 (\pm 0.05)	0.55 (\pm 0.05)	0.62 (\pm 0.09)	19.458	0.001
	Competitive	0.41 (\pm 0.04)	0.33 (\pm 0.03)	0.33 (\pm 0.03)	0.38 (\pm 0.01)	0.34 (\pm 0.04)	14.292	0.006
	Stress-tolerant	0.37 (\pm 0.04)	0.41 (\pm 0.12)	0.47 (\pm 0.07)	0.39 (\pm 0.03)	0.39 (\pm 0.03)	8.077	0.089
	Ruderal	0.33 (\pm 0.03)	0.37 (\pm 0.08)	0.32 (\pm 0.07)	0.35 (\pm 0.03)	0.38 (\pm 0.03)	3.867	0.424
	SLA	0.42 (\pm 0.03)	0.47 (\pm 0.08)	0.45 (\pm 0.05)	0.44 (\pm 0.02)	0.44 (\pm 0.03)	2.770	0.597
	Plant height	0.17 (\pm 0.08)	0.20 (\pm 0.09)	0.26 (\pm 0.11)	0.25 (\pm 0.04)	0.15 (\pm 0.02)	9.880	0.043
	Seed mass	0.20 (\pm 0.03)	0.17 (\pm 0.05)	0.14 (\pm 0.03)	0.17 (\pm 0.02)	0.15 (\pm 0.01)	12.714	0.013
	Clonality	0.21 (\pm 0.07)	0.17 (\pm 0.03)	0.43 (\pm 0.17)	0.64 (\pm 0.06)	0.65 (\pm 0.08)	22.017	0.000
	Taproot	0.59 (\pm 0.17)	0.57 (\pm 0.20)	0.28 (\pm 0.13)	0.32 (\pm 0.06)	0.32 (\pm 0.09)	13.897	0.008
	Perennial	0.46 (\pm 0.17)	0.49 (\pm 0.23)	0.72 (\pm 0.13)	0.86 (\pm 0.01)	0.80 (\pm 0.06)	19.471	0.001

4. Discussion

By applying the guild concept to the study of riparian herbaceous vegetation, as well as by directly studying variations in the mean value of individual traits, we highlighted the accumulated effects that anthropogenic stressors related to flow regulation and bedload transport can have on gravel bar plant communities. Specifically, we showed that the relatively stable riparian environment on the bypassed reaches of the Rhône River favored the development of hygrophilous species, with vegetative and perennial reproductive strategies, while the more dynamic and disturbed environment on the Drôme River favored the development of xerophilous species, with sexual and annual reproductive strategies. These results illustrated the environmental changes caused by flow regulation and altered bedload transport on riparian habitats and the functional response, in terms of life history (life cycle), reproductive strategy (clonality) and adaptation to drought stress (taproot), of plant communities. These results also revealed that the effects of anthropogenic stressors were cumulative in inducing a progressive shift in the values of ecological (light and soil moisture) and morphological (clonality and root type) traits shared by the species. This indicates that restoration actions targeting a single type of anthropogenic stressor will not be sufficient to direct riparian plant communities toward a near-natural reference state and that, therefore, there is an urgent need to develop more comprehensive actions based on the restoration of hydro-morphological processes at the scale of river reaches.

4.1. Increasing levels of anthropogenic stressors benefit perennial hygrophilous species guilds

In line with our hypotheses, our results showed that, for several guilds, species cover and redundancy increased or decreased with increasing levels of anthropogenic stressors. Indeed, of the six riparian guilds defined on the gravel bars of the Rhône, Drôme and Ain rivers, almost all varied significantly between the five river reaches studied. Specifically, pairwise comparisons revealed that statistically significant results were primarily related to comparisons between river reaches with greater differences in anthropogenic stressors, i.e., between, on the one hand, reaches with unregulated (DRM) or regulated (AIM) flow but with active bedload transport and, on the other hand, reaches with regulated and stabilized baseflow with inactive bedload transport (PBN and DZM). Although many pairwise comparisons were not significant, likely due to the small size of our sample, a progressive shift in the representativeness of several guilds with increasing levels of anthropogenic stressors was graphically demonstrated. As evidenced by previous studies (e.g., Bejarano *et al.*, 2018; Aguiar *et al.*, 2018; Su *et al.*, 2020), these results confirm that flow and bedload alterations due to damming, combined in the case of the Rhone with stabilization of baseflow during the growing season, lead to changes in species shared set of traits.

Our results highlighted in particular that species cover and redundancy in guild 4, i.e., xero-oligotro-taproot species, and guild 5, i.e., mesoxero-mesotro-taproot species, were significantly higher in the unregulated Drôme River. These results diverge from those found in Mediterranean regions, where the representativeness of related woody guilds, i.e., the 'xeric' guild (Bejarano *et al.*, 2012) and the 'Mediterranean evergreen' guild (Aguiar *et al.*, 2018), tend to increase in response to flow alteration. However, in these studies, flow alteration was related to water declines, whereas in the Rhone system, it was related flow stabilization. Overall, this combination of traits suggests that rivers with more stressful, nutrient-poor environmental conditions benefit

drought-adapted species with deeper root systems (i.e., allowing connection to groundwater sources). Indeed, the Drôme is a Mediterranean river whose baseflow is not sustained by dam releases and where dry summers can lead to a flow interruption for several weeks. Most of the pioneer species that characterize guild 3, i.e., meso-euro-annual taproot species, however, did not vary significantly between reaches. This indicates that even in highly anthropized rivers, and likely due to mechanical clearing of vegetation for flood risk management (Janssen *et al.*, 2022a), pioneer plant communities can still find riparian habitats in which to establish, as evidenced on low-lying bars made up of coarse-grained sediments and more frequently flooded in the bypassed reaches of the Rhône River (Janssen *et al.*, 2022b).

Conversely, our results showed that, on the Rhône, regulated reaches with a stabilized baseflow, and even more so those managed by plowing (i.e., DZM), promoted a greater species redundancy in guild 1, i.e., hygro-perennial tall species, and guild 2, i.e., hygro-perennial clonal species, and, to a lesser extent, to a higher cover of species in guild 6, i.e., meso-euro-perennial species. In northern Sweden, Bejarano *et al.* (2018) also reported that species redundancy in the 'deciduous wetland plants' guild increased on the most regulated boreal rivers. Furthermore, the cover of the 'flood-tolerant riparian herbs' guild was shown to increase in response to prolonged flooding conditions in China (Su *et al.*, 2020). This combination of traits suggests that flow regulation and stabilization associated with limited sediment supply conditions have promoted less stressful, more stable, and more fertile abiotic conditions (Franklin *et al.*, 2009; Janssen *et al.*, 2021) and the development of medium to tall, often clonal, perennial species (e.g., Minchinton & Bertness, 2003; Chen *et al.*, 2017), better adapted to competitive interactions because less subject to environmental selection. Although these results can be partially explained by differences in gravel bar topography and soil texture between the five river reaches studied, they also reflect differences and adaptations that can be more directly attributed to anthropogenic environmental changes. Thus, in addition to stabilized baseflows, bedload transport was shown to be limited to fine-grained sediments in the Pierre-Bénite (PBN) and Donzère-Mondragon (DZM) bypassed reaches (Vázquez-Tarrío *et al.*, 2019). Coupled with the lateral stability of bars, our results suggest that in the absence of major flood events, the burial and scouring disturbance processes that allow for the destruction of plant biomass (Kui & Stella, 2016) and renewal of riparian habitats can no longer occur on the most anthropized reaches of the Rhone. This promotes silt deposition on aging gravel bars often fixed by groynes (i.e., transversal dikes), which locally increases substrate water holding capacity and nutrient availability (Franklin *et al.*, 2009; Asaeda & Rashid, 2012) to the benefit of hygrophilic, mesotrophic perennial vegetation but at the expense of xerophilic species adapted to drought stress.

4.2. Individual traits analysis highlighted the effects of anthropogenic stressors on the ecological preferences of communities and associated morphological adaptations

Consistently with the results reported using the guild approach and the hypotheses made, variations in the mean value of individual traits were mainly related to ecological preferences and morphological traits of species. However, taking into account the values of the Kruskal-Wallis H-statistic, it appears that clonality was the trait that most responded to variations between river reaches, followed by light requirements, life form and soil moisture requirements. This information allows us to more clearly highlight changes in environmental

conditions between reaches, as shown by variations in species' ecological preferences (Ellenberg *et al.*, 1992), as well as the adaptative response of plants to these changes, as indicated by several morphological traits. Thus, communities established on unregulated reaches with active bedload transport included more species adapted to full light (heliophilous) and dry (xerophilous) conditions than those on regulated reaches with inactive bedload transport but not more species adapted to nutrient-poor environments (oligotrophilous), as suggested by the guild approach. It can therefore be inferred that the five river reaches studied represent increasing levels of drought, more likely due to the fluctuating, downwelling low-water hydrology on the unregulated reaches than to fine sediment deposition on the regulated reaches. Indeed, although statistically significant variations in soil texture properties were measured between reaches, the magnitude of these variations was not very large. Therefore, with the exception of the more elevated and disconnected quadrats, where the proportion of fine sediments was greater than 50 % in all five river reaches, most of the plant communities sampled were established on coarse-grained sediments but subject to different flow regimes. This is well illustrated by the hydrographs of the five river reaches, which show fairly comparable high and low water regimes over the study period but a different frequency, i.e., characterized by long periods of stable flows with occasional flood peaks on the three Rhône reaches (MRJ, PBN, DZM). This stabilization of baseflows limits the intensity of drought events due to lowering of water levels in summer (Poff *et al.*, 2007), as is still the case for the Drôme and to a lesser extent the Ain, and allows the development of hygrophilous species in environmental conditions close to those encountered in lentic environments (Cronk & Fennessy, 2001). In response to these variations in drought levels, which decreased with the accumulation of anthropogenic stressors, variations in species traits clearly showed a shift in life history, from annual to perennial species, reproductive strategies, from sexual to vegetative, and morphological adaptations for water resource access, from taproots to fibrous roots. This effect on a set of shared traits was consistent with changes in species ecological preferences measured between near-natural and highly degraded gravel bars and matched known morphological adaptations of plant communities between dynamic riparian habitats and stable wetlands (Cronk & Fennessy, 2001; Merritt *et al.*, 2010; Diehl *et al.*, 2017; Vesipa, Camporeale & Ridolfi, 2017). Indeed, plant communities established on mobile and frequently flooded gravel bars are subject to severe physical constraints, including erosion and burial disturbances that limit vegetation encroachment from year to year (Friedman *et al.*, 2022), but also to prolonged summer droughts that favor environmental selection towards plant species either deeply anchored in the sediments (Stromberg, 2013) or completing their life cycle over a few months (Reynolds & Shafroth, 2017). In contrast, fixed gravel bars, even when frequently flooded, are more stable riparian habitats that allow for the development of perennial species that progressively dominate communities through the spatial dynamic of the lateral spread of ramets (Friedman *et al.*, 2022). However, contrary to what the guild approach suggested, plant height at maturity was not a morphological trait that responded to increasing levels of anthropogenic stressors. This indicates that the higher cover and redundancy of species in guild 1 i.e., hygro-perennial tall species, was not large enough to induce significant variation in the mean plant height value when considering the gravel bar species pool, i.e., the cover of several small and medium perennial clonal species also increased with increasing levels of anthropogenic stressors (e.g., *Cynodon dactylon*, *Ludwigia peploides*, *Trifolium repens*).

Individual trait analysis also revealed that, contrary to our hypotheses, CSR strategies and SLA values of riparian plant communities were overall not or slightly influenced by differences in flow and sediment regimes among the five river reaches studied. This is likely due to the fact that species from the four quadrats were pooled together at the transect scale and thus variations in species composition and traits along the lateral gradient of connectivity were not considered in this study. Since plant acquisitive and conservative strategies are known to be strongly shaped by elevation differences from the waterline (see e.g., Kyle & Leishman, 2009; McCoy-Sulentic *et al.*, 2017; Oddershede *et al.*, 2019; Janssen, Piégay & Evette, 2020), these results may suggest that local topographic variables are more important than reach scale anthropogenic stressors in explaining average variation in species ecological strategies and related morphological traits.

5. Conclusion

By studying variations in species cover and redundancy of six riparian guilds, as well as the mean value of twelve ecological and morphological traits, along increasing levels of anthropogenic stressors on gravel bars, we showed (1) that there is a cumulative effect of flow regulation and altered bedload transport on the functional response of herbaceous plant communities, and (2) that human modifications of the hydrogeomorphic regime of rivers have induced changes in a set of shared traits, orienting riparian communities toward a dominance of perennial hygrophilic clonal species. These results revealed that environmental changes induced by human infrastructures have strong effects on species ecological niche, mainly by reducing the intensity of drought and homogenizing the variability of river flow in our study system, which in response result in morphological adaptations of the riparian vegetation. Since the highlighted response traits can be linked to effect traits that affect flow turbulence and sediment deposition (Diehl *et al.*, 2017), it is likely that morphological changes induced by human activities in turn promote biogeomorphological interactions that may further decrease the intensity of drought (Corenblit *et al.*, 2009). For example, our results showed that the abundance of perennial and clonal species in the communities increased in response to flow regulation and stabilization, thereby promoting the biomass production process on the gravel bars. This leads to densification, stabilization and homogenization of the vegetation cover with expected effects on the soil erosion control service, i.e., by protecting the bank and increasing the trapping of fine sediments, but also on the biodiversity support service, i.e., by decreasing the diversity of plant species, as shown by complementary studies on the Rhône River (Janssen *et al.*, 2020, 2022b). This shift from response traits to effect traits, together with an understanding of the related processes, is however made possible by the individual analysis of variations in mean trait values. Indeed, although the guild approach allowed us to construct groups of species that responded consistently to anthropogenic stressors, the individual trait approach allowed us to disentangle more clearly between the response of plant communities related to the ecological requirement of species and their morphological adaptations. Thus and in addition to the fact that the results related to the guild approach are difficult to compare across studies due to differences in trait selection and guild naming (Lozanovska *et al.*, 2018), we argued that the analysis of individual traits provides a useful source of information to gain a more mechanistic and reproducible understanding of the effects of human-induced stressors on riparian community

structure. There is therefore a strong interest in complementing the guild approach with the study of individual traits (see e.g., Stromberg & Merritt, 2016).

Finally, and from an applied point of view, our results showed that the restoration actions targeting a single stressor will not be sufficient to reorient riparian plant communities towards an ecological state closer to reference systems. For example, on the Rhône River, the accumulation of human-induced stressors over time, i.e., a correction phase during the 19th century followed by a derivation phase in the second half of the 20th century, have deeply altered the flow and sediment regime of this large river (Vázquez-Tarrío *et al.*, 2019; Tena *et al.*, 2020) as well as the associated riparian communities (Janssen *et al.*, 2021). Thus, even if lateral bank erosion will certainly be enhanced by actions at the site scale, such as with the removal of lateral dikes, the reactivation of the fluvial dynamics allowing the recreation of pioneer habitats will require a more integrated approach based on the restoration of hydrological, morphological and ecological processes at the reach scale. In highly anthropized rivers, this implies implementing complementary restoration actions, i.e., re-establishing a flow regime more in line with natural flow variations upstream of the dams and reactivating bedload transport by carrying out gravel augmentation. Taken together, these actions should promote the expression of rejuvenated processes, either by scour and burial disturbances, and thus allow for the expression of a wider diversity of riparian plants communities and habitats.

6. Author contributions

Conceptualisation: AE, CC, HP, PJ. Developing methods: CC, PJ. Conducting the research: CC, PJ. Data analysis: CC, PJ. Data interpretation: AE, CC, HP, PJ. Preparation of figures and tables: CC, PJ. Writing: AE, CC, HP, PJ.

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9. Conflict of interest statement

The authors declare no conflict of interest.

10. Data availability statement

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

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