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RESEARCH ARTICLE

Influence of local environmental gradients on ecological strategies of herbaceous communities in riverine side channels

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Abstract

Questions: In riverine side channels (secondary and former arms), the alternation of lotic, lentic and dry phases produces disturbance and resource gradients that filter species and community strategies. To better understand the impact of this alternation of functioning on plant communities at a fine spatial scale, we tested for the effects of elevation (linked to water level), slope, longitudinal position, light availability and sediment grain size on (i) taxonomic composition and (ii) competition, stress tolerance, and ruderal strategies (C, S and R strategies) at the community level. We hypothesized that fewer resources would increase the stress-tolerant prevalence (i.e., community-weighted mean value), while topographic gradients would affect ruderal prevalence. In addition, we hypothesized that strong and directional environmental filtering should reduce the co-occurrence of species with different CSR strategy values (i.e., low C, S and R functional dispersion).

Location: Fourteen side channels on the lower reach of the Loire river (France).

Results: Taxonomic composition of the herb layer and environmental variables were assessed on 474 plots. The relations between species composition and environmental gradients were investigated by a constrained analysis of principal coordinates. The effects of environmental gradients on community CSR strategies were assessed using mixed-effects models and a model-averaging procedure.

Results: Taxonomic community composition was shaped mainly by light availability, topographic elevation and sediment grain size. Slope and the interaction between light and elevation influenced the community-weighted mean and functional dispersion values of S and R strategies. Among other interactions, those involving sediment grain size shaped the dispersion values for C and R strategies.

Conclusion: The study identified shading and fine sediment grain size as key drivers of biotic homogenization in the riverscape. Increasing the disturbance frequency and magnitude would limit the progression of the ecological succession and favor the co-occurrence of taxonomically and functionally diverse communities within the side channels.

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KEYWORDS

alluvial ecosystems, environmental filters, functional dispersion, Grime's CSR strategies, riparian zone, river management, strategy co-occurrence, terrestrialization process

1 | INTRODUCTION

The study of the distribution of species along environmental gradients allows understanding which parameters most influence community structure. However, analyzing communities with regard to species composition does not enable comparison of the effects of similar processes between distant sites, for example, sites with different species pools (Mcgill et al., 2006). To move beyond the species-based approach, functional-trait-based approaches have been developed (Lavorel & Garnier, 2002). They are based on the fact that trait values vary along environmental gradients in a predictive way (Shipley et al., 2016). Recently it has been shown that plant strategies as proposed by Grime (1977), that is, competitive, stress-tolerant and ruderal strategies (C, S and R strategies) can be studied by focusing on only three leaf traits that represent morphological–physiological trade-offs (Pierce et al., 2012; Pierce et al., 2017). The first, leaf area (LA), reflects the plants' ability to intercept light and has been shown to be moderately correlated with plant size (Díaz et al., 2004; Díaz et al., 2016; Kleyer et al., 2019). It is therefore related to competitive ability. The second, leaf dry matter content (LDMC), indicates nutrient allocation patterns and biomass turnover rate. Low LDMC is associated with a high growth rate that is typical of the ruderal strategy. The third, specific leaf area (SLA) reflects the maximum photosynthetic ability and the relative growth rate: low SLA values are indicative of stress adaptation. The SLA/LDMC balance represents the economic spectrum, which is a trade-off between acquisitive (high biomass turnover) and conservative (defense investment) leaf functioning (Wright et al., 2004; Pierce et al., 2012). Thus, the leaf economic spectrum is indicative of stress and disturbance adaptations.

To understand how environmental gradients shape the structure and dynamics of plant communities, it is useful to study average trait values within communities and their variations. Average trait value reflects the adaptation to environmental gradients. Dispersion around the average value indicates trait convergence or divergence within the community. At the local scale, environmental filtering and biotic interactions (e.g., competitive exclusion) may result in functional convergence (i.e., a narrow range of trait values), while functional divergence (i.e., a broad range of trait values) may result from limiting similarity mechanisms or disturbances (Grime, 2006; Bernard-Verdier et al., 2012; Backhaus et al., 2021; de Bello et al., 2013). These two dimensions of community trait variation can be explored using both community-weighted mean (CWM, Lavorel et al., 2007) and functional dispersion (FDis, Laliberté et al., 2014). Placed back into the predictions of Grime's CSR theory, it has been shown, both experimentally (Li & Shipley, 2017) and empirically (e.g., Janssen et al., 2020; Escobedo

et al., 2021), that changes in the community-weighted mean values and functional dispersion values of competitive, stress-tolerant and ruderal strategies adequately reflect observed variations in stress and disturbance levels.

Worldwide, most large rivers are human-impacted by fragmentation, regulation or sediment mining (see e.g., Grill et al., 2019). In general, those modifications alter the functioning of fluvial features such as side channels, and their ability to support typical riparian ecosystems and related plant communities (Naiman et al., 1993; Richardson et al., 2007). Erosion/deposition processes and hydrological connectivity exert strong filtering on non-woody communities in alluvial ecosystems (Zelnik & Čarni, 2008; Su et al., 2020; Janssen et al., 2022). Fluvial side channels (i.e., secondary channels and former main or secondary channels) are more or less connected to the main river channel. Their hydrological connectivity encompasses a broad range of flood characteristics such as continuous or intermittent running, slow-flowing, standing water, and absence of water (Petts & Amoros, 1996; Tockner et al., 1999; Pringle, 2001; Pringle, 2003). Side channels moreover host a variety of morphological units (e.g., ponds, bars, banks, etc.) that present a diversity of environmental conditions for plants to establish and for fluvial biogeomorphological succession to occur (Garófano-Gómez et al., 2017; Greulich et al., 2019; Tabacchi et al., 2019). Therefore, they concentrate strong gradients of stress and disturbance over limited spatial areas (Gregory et al., 1991). Within this context, stress levels may be driven by the resource gradients, that is, light and nutrient availability. Both are functions of canopy closure and sediment grain size respectively (Greulich et al., 2000; Zenner et al., 2012). The disturbance level may rely on topographical gradients such as slope and elevation relative to flowing water but also proximity to the main channel. Disturbance can be expected to be strong at low elevation and close to the main channel—especially in the upstream part of the side channel where flow turbulence is maximum (Claude et al., 2014), or at very steep locations resulting from erosion processes (Kyle & Leishman, 2009; O'Hare et al., 2016). All gradients may represent environmental filters that select trait range and species suited to grow under specific site conditions (Fraaije, ter Braak, Verduyn, Breeman, et al., 2015; Hough-Snee et al., 2015; Soons et al., 2017). Stress and disturbance gradients can also interact and induce shifts in the ecological strategies deployed by plant species, as demonstrated on gravel bars subjected to fine-sediment deposition (Janssen et al., 2020). Moreover, changes in species composition do not always result in significant changes in functional traits when local abiotic conditions are similar over years (Janssen et al., 2022).

The present study aims to understand the effects of structuring environmental gradients—light and hydrosedimentary connectivity—on the species composition and ecological strategies of herbaceous communities within side channels of a large river. We



hypothesize that resource and topographical gradients (as proxies of disturbance level) affect the community composition. Then, based on Grime's CSR theory, we more specifically test the following three hypotheses at the community scale: (1) increasing light availability and decreasing sediment grain size should reduce the stress level and thus induce a decrease in the mean value of stress tolerators (i.e., low S_{CWM}); (2) high elevation, gentle slope and proximity to the downstream end of the side channel should reduce the disturbance level and induce a decrease in the mean value of ruderals (i.e., low R_{CWM}); (3) a lowering of stress and disturbance levels should induce an increase in the mean value of competitors (i.e., high C_{CWM}). In addition to studying changes in the mean values (i.e., community-weighted mean) of CSR strategies, we investigated how the co-occurrence of species with different CSR strategy values (i.e., functional dispersion) varied within communities as a function of the intensity of environmental filters. Specifically, we hypothesized that (4) strong and directional environmental filtering should induce a decrease in the co-occurrence of species with different CSR strategy values (i.e., low CSR_{FDIS}); and (5) intermediate positions along environmental gradients, related to more heterogeneous habitat conditions, should induce an increase in the co-occurrence of species with different CSR strategy values (i.e., high CSR_{FDIS}). Finally, (6) we expect the ecological strategies of plant communities to respond non-independently to variations in environmental parameters (e.g., interaction between light availability and elevation level).

2 | METHODS

2.1 | Study sites

The study took place in the lower reach of the Loire river (France), from the confluence with the Vienne river (Montsoreau) to the confluence with the Sèvre nantaise river (Nantes) (Figure 1). The reach is about 140 km long with a mean slope of 0.2 m km^{-1} . The fluvial style is mainly multiple channels, separated by large vegetated islands. The bedload is sandy/gravelly ($d_{50} = 0.90 \text{ mm}$, Le Guern et al., 2021) and consists of siliceous material. The river along the study reach presents a mean annual discharge of $839 \text{ m}^3 \text{ s}^{-1}$, the inter-annual maximum flood discharge is $2710 \text{ m}^3 \text{ s}^{-1}$ and the inter-annual minimum low-flow discharge is $160 \text{ m}^3 \text{ s}^{-1}$ at the Montjean-sur-Loire gauging station (calculated from 1863 to 2021, "Banque Hydro" database, 2021, <http://www.hydro.eaufrance.fr>). Tidal influence increases from Saint-Florent-le-Vieil to the estuary. Climate is temperate under oceanic influence, the latter increases from upstream to downstream along the river course. The mean annual precipitation is 709.3 mm and normal annual temperature is 12.6°C at the Beaucouzé meteorological station (1991–2020; Météo-France, 2023, <https://donneespubliques.meteofrance.fr>).

Among 92 side channels identified along the study reach of the Loire, 14 side channels were selected based on their morphological attributes (i.e., length:width ratio [10;300]), geographical situation (regular distribution along the reach), and amount and dynamics

of the tree layer groundcover between 2002 and 2012 (Figure 1, Appendices S1 and S2). This subset is considered representative of the whole range of partly disconnected side channels of the lower Loire river.

The side channels shelter a broad range of habitats including aquatic and helophytic formations, herbaceous communities on sediment bars and riverbanks such as dry, seasonally wet and wet grasslands, as well as riparian forests dominated by *Salix* spp. or *Fraxinus angustifolia*.

2.2 | Vegetation survey

For each side channel ($n = 14$), vegetation surveys were conducted in late July 2019 ($n = 5$) and late July 2020 ($n = 9$). Within each side channel, 6–10 transversal transects of various lengths (depending on channel width, accessibility and the presence of riprap, mean = 31 m, SD = 16) were regularly spaced. Along each transect, depending on available space, 3–5 quadrats of $2 \text{ m} \times 2 \text{ m}$ (4 m^2 plot) were regularly positioned, while respecting a minimal distance of 5 m between them. In each plot, the presence of all vascular plant species within the herb layer (except woody seedlings) was recorded and species groundcover was assessed using the abundance–dominance index (Braun-Blanquet, 1928 in Loïc, 2015). Plots with a slope superior to 70° , as well as aquatic plots (i.e., under water at the time of the survey), were not considered in the following analysis because they were few in numbers and had very low plant cover and species numbers. Some plots that were grazed were dismissed too. Finally, the retained data set included 474 plots and a total of 155 taxa (Appendix S3). All vegetation surveys were conducted by the first author. Nomenclature followed the taxonomic referential Taxref.v14 (Gargominy et al., 2020).

Species strategies were assessed via the traits LA, LDMC and SLA. Trait values were extracted from the TRY database (Kattge et al., 2019, public data only) and filtered (i.e., risk error ≤ 3) before averaging. CSR strategy scores for 96 species were then calculated with the StrateFy tool (Pierce et al., 2017, in their Supplementary Material S2), by using the mean values of leaf traits. The tool derives species' C, S and R scores on the basis of a principal component analysis (PCA) that uses normalized LA, LDMC and SLA distributions of a worldwide set of species ($n = 3068$) as a calibration set. If leaf traits were missing, CSR scores were either collected from Pierce et al., 2017 (in their Supplementary Material S1) for 33 species, or taken from a closely related taxon (i.e., same genus, $n = 9$), or, whenever possible, calculated by averaging available values of species from the same genus and known in western France (Bousquet et al., 2015) ($n = 10$, Appendix S3). CSR scores were missing for seven species (*Arum italicum*, *Butomus umbellatus*, *Cuscuta campestris*, *Mollugo verticillata*, *Scrophularia auriculata*, *Silene baccifera* and *Solanum nigrum*) which represent about 1.55% of the total number of plant records ($n = 2897$). CWM and functional dispersion (FDIS) were then computed for each plot and each strategy using the "dbFD" function.

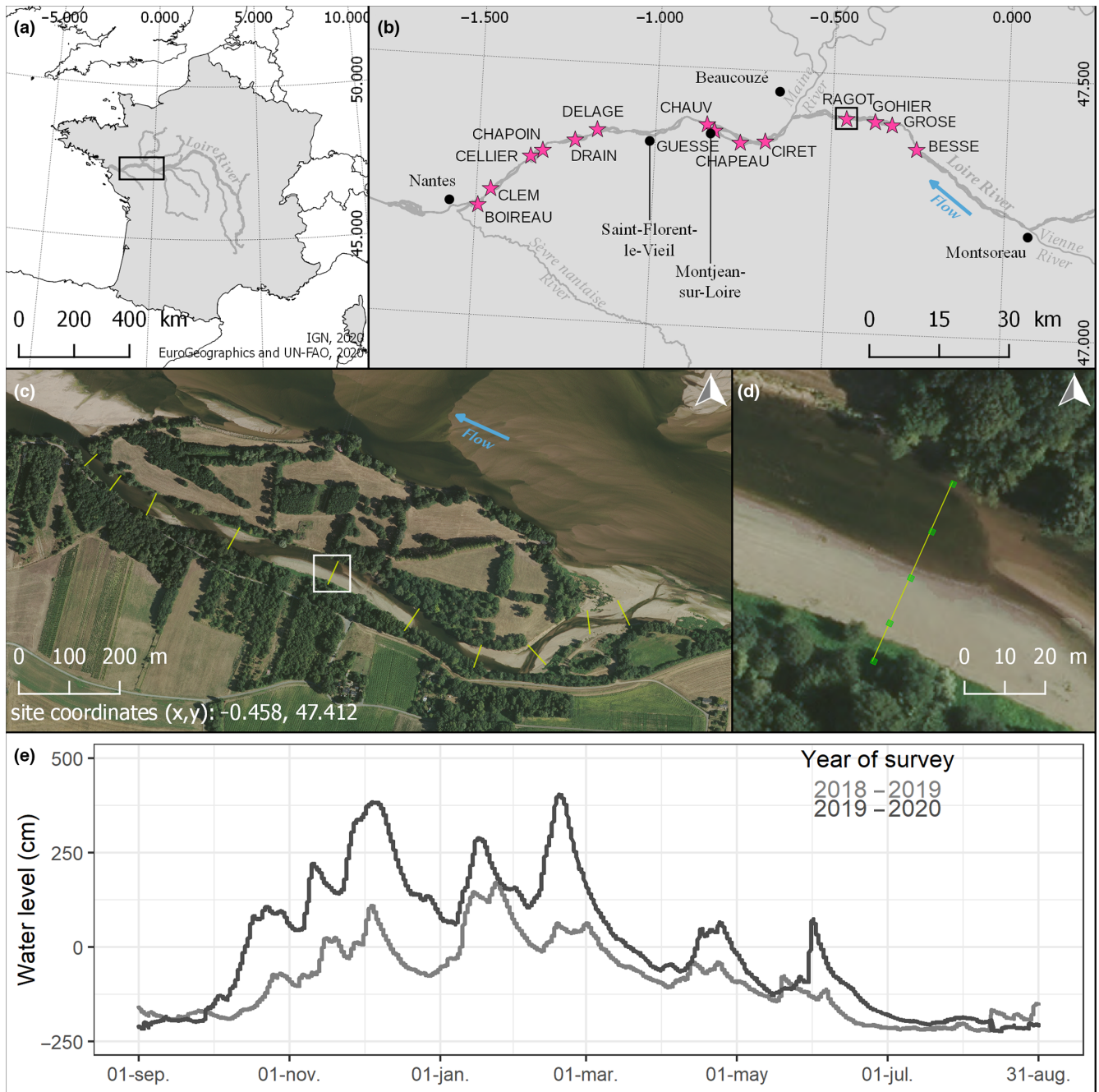


FIGURE 1 Study reach, study sites and sampling patterns (BD_TOPO®, BD_ORTHO®). (a) Location of the lower Loire river in France; (b) study sites (stars) along the study reach; (c) study site “le bras du Ragot” and sampling transects; (d) sampling transect and sampling plots; (e) mean daily water level during the years of survey at the gauging station of Montjean-sur-Loire.

2.3 | Environmental parameters

In each quadrat, geographic position, canopy openness, dominant sediment grain size classes and slope of the plot (perpendicular to the talweg) were recorded in situ. The 3D coordinates were determined with a centimeter-precision GPS, and two parameters were calculated using QGIS (version 2.18, QGIS Development Team, 2016). First, elevation relative to the water level (hereafter *elevation*) was interpolated from a digital elevation model at

low-flow water level (September 17 and 18, 2017; water level at Montjean-sur-Loire = -1.60 m). Second, to take into account a plot's position within the side channel, we calculated the relative distance of each plot from the downstream end to the upstream end (hereafter *distance*, 0 = downstream end, 1 = upstream end). At the center of each plot, canopy openness (hereafter *light*) was measured using a spherical convex densiometer at 1.60 m height. Dominant grain size classes of sediment (hereafter *grain size*) were assessed visually after one auger sampling of the top layer



(0–10 cm) and was summarized into a numerical index. We assigned a score to the primary dominant grain size classes (i.e., 1 = clay and organic matter, 2 = silts, 3 = sands, 4 = pebbles, 5 = rocks). If a second dominant grain size class was observed, 0.5 was added to the score when the particle size of the sediment was coarser than the first one, or 0.5 was subtracted when it was finer. The slope of the plot (hereafter *slope*) was assessed visually into three classes ([0,5], [5,30], [30,70], in degrees) and turned into a numerical index ranging from 1 to 3 respectively.

Because our study focuses solely on the effects of local environmental gradients, longitudinal gradients along the Loire river, that is, tidal and climatic influences, were assessed but only used as covariates in the subsequent analyses. Tidal amplitude (hereafter *tide*) was calculated based on the mean daily tidal amplitude (m) by interpolation from the closest gauging stations for each side channel (hereafter *site*) at the hydroperiod of the relevé (Banque Hydro, 2021, <https://www.hydro.eaufrance.fr/>). Both annual cumulated rainfall and annual mean temperature (hereafter *rainfall* and *temperature*) were extracted for each site at the hydroperiod of the relevé from the Safran-Isba-Modcou model (MétéoFrance, 2021, <https://publithèque.meteo.fr/>).

2.4 | Statistical analysis

To test whether environmental parameters influence the species composition in side channels, we used forward model selection (“ordistep” function) on the distance-based redundancy analysis (dbRDA, “capscale” function). To avoid overdispersion, 69 species were removed from the analyses (occurrence inferior to 5). A dissimilarity matrix was generated based on Bray–Curtis distance calculation, and distances were square-root-transformed to avoid negative eigenvalues. To reduce the unconstrained proportion of inertia, *tide*, *rainfall* and *temperature* were considered as covariates. The number of permutations was set to 499, and they were restricted within *sites*. The full model used *light*, *elevation*, *grain size*, *slope* and *distance* to constrain the total inertia. To test if each environmental variable played a significant role in structuring communities, we used a permutation test (“anova.cca” function) set by margin. Dissimilarities in species compositions among communities were visualized by using a partial constrained analysis of principal coordinates (CAP), in which CWM and FDis scores for C, S and R strategies were also represented (“envfit” function).

To test which environmental parameters shape ecological strategies of herbaceous plants at the community level, that is, C_{CWM} , S_{CWM} , R_{CWM} , C_{FDis} , S_{FDis} , and R_{FDis} , we used a modeling approach. We developed a set of 71 a priori models, which integrated from one to five environmental parameters without interaction or included a maximum of three variables when an interaction was taken into account (Appendix S4), plus a null model. To control for tidal influence and climatic gradients along the river reach and inter-annual variations between sampling years, related covariates were integrated in all a priori models. Moreover, because quadrats

within a side channel were not independent replicates, we included site as a random effect. Numerical explanatory variables were centered and scaled and checked for lack of inter-correlation ($-0.5 < r < 0.5$, Appendix S5). Because we were interested in the comparison and combination of several candidate models, they were fitted with response variables using the “lmer” function and estimates were computed by maximum likelihood. To avoid collinearity issues, the variance inflation factor was checked within each model for the six response variables (“vif” function); none was superior to three. The explained variance for the fixed effect was estimated using marginal R^2 (“r.squaredGLMM” function). We used Akaike’s Information Criterion corrected for small samples (AICc) to rank the models and identify the most parsimonious, and the Akaike weight was calculated for each candidate model (“model.sel” function). Estimates of the parameters and unconditional standard errors were obtained through model averaging, by taking into account as many models as necessary to obtain a 0.95 cumulated Akaike weight (“model.avg” function).

Analyses were performed within the R environment (version 3.6.1, R Core Team, 2019) using “car” (Fox & Weisberg, 2019), “FD” (Laliberté et al., 2014), “lme4” (Bates et al., 2015), “MuMin” (Barton, 2020), and “vegan” (Oksanen et al., 2019) packages.

3 | RESULTS

3.1 | Effects of environmental gradients on taxonomic composition and strategy distribution

The partial dbRDA which had the lowest AIC was the full model integrating the five environmental variables *elevation*, *light*, *grain size*, *slope* and *distance*. Constrained inertia (i.e., environmental variables) explained 4.13% ($F_{5,464} = 4.152$, $p = 0.002$) of the total inertia and conditional inertia (i.e., covariates) accounted for 3.57%. Three among five axes were significant in the constrained analysis of principal coordinates (CAP, with respectively $F_{1,464} = 11.430$, $p = 0.002$; $F_{1,464} = 3.792$, $p = 0.002$; $F_{1,464} = 2.656$, $p = 0.002$). All variables had a significant influence on the taxonomic composition of side channels (*light*: $F_{1,464} = 3.436$, $p = 0.002$; *elevation*: $F_{1,464} = 3.276$, $p = 0.002$; *grain size*: $F_{1,464} = 3.593$, $p = 0.002$; *slope*: $F_{1,464} = 2.566$, $p = 0.002$; and *distance*: $F_{1,464} = 2.283$, $p = 0.002$). Within the constrained inertia, relative elevation above the water level and slope were negatively correlated with axis 1 of the CAP, while light availability was positively correlated (Figure 2a). Regarding ecological strategies (Figure 2a), mean and dispersion values for stress tolerators were mostly related to CAP axis 1, in the same direction of elevation and slope gradients. Ruderal mean values were opposite to S-traits on axis 1, in the direction of the light gradient. Functional dispersion for ruderals and competitors were better aligned with axis 2. Competitor mean values did not fit the ordination significantly. Therefore, the first CAP axis opposed plots with low light conditions, situated at rather high elevation and hosting terrestrial and/or understorey species such

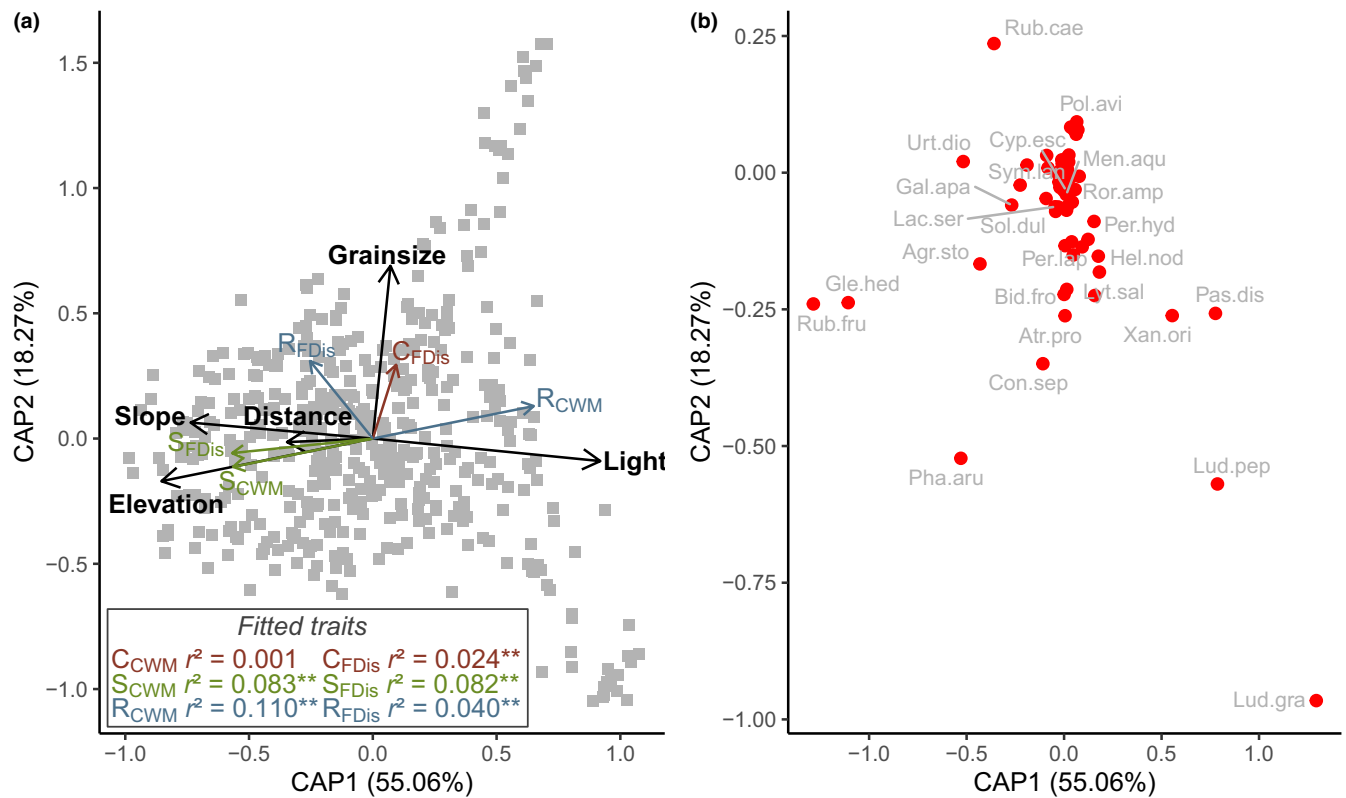


FIGURE 2 Ordination of sampling plots by constrained analysis of principal coordinates (CAP). (a) Biplot of sampling plots on principal component axes and correlation of environmental variables on which competitor (C), stress tolerator (S) and ruderal (R) community-weighted mean (CWM) and functional dispersion (FDIs) were fitted: gray squares, sampling plots; black arrows, scores of environmental variables (multiplied by 3); colored arrows, scores of fitted strategy parameters (multiplied by 2); r^2 , fitting with CAP; and **, significant fitting ($p < 0.01$). (b) Species ordination, labels of the 25 most frequent species are displayed (Agr.sto = *Agrostis stolonifera*, Atr.pro = *Atriplex prostrata*, Bid. fro = *Bidens frondosa*, Con.sep = *Convolvulus sepium*, Cyp.esc = *Cyperus esculentus*, Gal.apa = *Galium aparine*, Gle.hed = *Glechoma hederacea*, Hel.nod = *Helosciadium nodiflorum*, Lac.ser = *Lactuca serriola*, Lud.gra = *Ludwigia grandiflora*, Lud.pep = *Ludwigia peploides*, Lyt. sal = *Lythrum salicaria*, Men.aqu = *Mentha aquatica*, Pas.dis = *Paspalum distichum*, Per.hyd = *Persicaria hydropiper*, Per.lap = *Persicaria lapathifolia*, Pha.aru = *Phalaris arundinacea*, Pol.avi = *Polygonum aviculare*, Ror.amp = *Rorippa amphibia*, Rub.cae = *Rubus caesius*, Rub.fru = *Rubus fruticosus*, Sol.dul = *Solanum dulcamara*, Sym.lan = *Symphotrichum lanceolatum*, Urt.dio = *Urtica dioica* and Xan.ori = *Xanthium orientale*).

as *Glechoma hederacea* and *Rubus fruticosus* (s.l.), to plots with high light conditions located at lower elevations (Figure 2b). Sediment grain size was positively correlated with the second CAP axis, opposing plots made of coarse-grained sediments characterized by the larger co-occurrence of fluvial pioneer species (i.e., species occurring on sediments bars) to plots with fine-grained and organic sediments, comprising the invasive amphiphytes *Ludwigia peploides* and *Ludwigia grandiflora* (Figure 2b). Finally, the distance from the downstream end to the main channel was best correlated with the third CAP axis (figure not shown).

3.2 | Effects of environmental gradients on ecological strategies

The top-ranked models predicting variations in the mean and dispersion values of CSR-traits explained between 6.7% and 22.3% of the variance (Appendix S6). Since the null model was the best to explain the mean competitor values (C_{CWWM}), none of the parameters chosen

to describe the local environmental gradients of the side channels can be considered to have any inferential value.

3.3 | Effects of environmental gradients on the mean values of ecological strategies

Model averaging revealed that *slope* had a significant positive effect on the mean values for stress tolerators (S_{CWWM}) (Table 1). S_{CWWM} was also significantly influenced by the interaction between *light* and *elevation*, that is, shade conditions mitigated the increase in S_{CWWM} values along the elevation gradient (Figure 3b), and between *elevation* and *distance*, that is, the upstream position within the channel mitigated the increase in S_{CWWM} values along the elevation gradient (Figure 4b). *Slope* had a significant negative effect on the mean values of ruderals (R_{CWWM}). The interaction between *light* and *elevation* was significant, that is, while R_{CWWM} decreased along the elevation gradient in high light conditions, it remained stable in shade conditions (Figure 3c).

TABLE 1 Model averaging of community-weighted mean (CWM) for C (competitive), S (stress-tolerant) and R (ruderal) strategies.

Parameters	CWM C		59		CWM S		21		CWM R		2	
	Imp.	n =	Estimate (\pm SE)	(95% CI)	Imp.	n =	Estimate (\pm SE)	(95% CI)	Imp.	n =	Estimate (\pm SE)	(95% CI)
Tide	1.00		0.112 (\pm 0.910)	(-1.671; 1.894)	1.00		-1.625 (\pm 1.353)	(-4.277; 1.027)	1.00		2.051 (\pm 0.853)	(0.378; 3.723)
Rainfall	1.00		3.885 (\pm 0.917)	(2.087; 5.684)	1.00		0.388 (\pm 1.360)	(-2.277; 3.054)	1.00		-4.213 (\pm 0.850)	(-5.879; -2.547)
Temperature	1.00		0.285 (\pm 0.921)	(-1.521; 2.090)	1.00		0.551 (\pm 1.379)	(-2.152; 3.254)	1.00		-0.799 (\pm 0.857)	(-2.479; 0.881)
Light	0.55		-0.702 (\pm 0.553)	(-1.787; 0.382)	0.50		-0.717 (\pm 0.753)	(-2.192; 0.758)	1.00		1.077 (\pm 0.671)	(-0.239; 2.392)
Elevation	0.35		0.448 (\pm 0.662)	(-0.849; 1.745)	1.00		2.534 (\pm 0.922)	(0.726; 4.342)	1.00		-3.857 (\pm 0.786)	(-5.397; -2.317)
Grain size	0.34		-0.362 (\pm 0.630)	(-1.596; 0.872)	0.11		-0.456 (\pm 0.755)	(-1.936; 1.023)	NA		NA	NA
Distance	0.43		-0.478 (\pm 0.493)	(-1.444; 0.487)	0.36		0.477 (\pm 0.596)	(-0.692; 1.646)	NA		NA	NA
Slope	0.29		0.193 (\pm 0.530)	(-0.845; 1.232)	0.94		1.969 (\pm 0.658)	(0.679; 3.258)	0.95		-1.665 (\pm 0.577)	(-2.797; -0.533)
Light * elevation	0.08		0.955 (\pm 0.622)	(-0.264; 2.174)	0.36		1.970 (\pm 0.767)	(0.466; 3.473)	1.00		-2.863 (\pm 0.678)	(-4.192; -1.535)
Light * grain size	0.04		-0.524 (\pm 0.539)	(-1.581; 0.533)	NA		NA	NA	NA		NA	NA
Light * distance	0.04		0.032 (\pm 0.486)	(-0.920; 0.985)	NA		NA	NA	NA		NA	NA
Light * slope	0.03		0.379 (\pm 0.514)	(-0.628; 1.386)	0.01		-0.322 (\pm 0.617)	(-1.532; 0.887)	NA		NA	NA
Elevation * grain size	0.02		-0.541 (\pm 0.552)	(-1.623; 0.541)	0.01		0.614 (\pm 0.676)	(-0.711; 1.939)	NA		NA	NA
Elevation * distance	0.02		0.200 (\pm 0.494)	(-0.769; 1.168)	0.24		-1.547 (\pm 0.587)	(-2.697; -0.396)	NA		NA	NA
Elevation * slope	0.01		0.020 (\pm 0.474)	(-0.910; 0.950)	0.20		-1.009 (\pm 0.571)	(-2.128; 0.110)	NA		NA	NA
Grain size * distance	0.04		-0.673 (\pm 0.526)	(-1.704; 0.358)	NA		NA	NA	NA		NA	NA
Grain size * slope	0.01		0.205 (\pm 0.509)	(-0.791; 1.202)	0.01		-0.318 (\pm 0.612)	(-1.517; 0.881)	NA		NA	NA
Distance * slope	0.04		-0.583 (\pm 0.478)	(-1.520; 0.353)	0.01		-0.062 (\pm 0.575)	(-1.190; 1.066)	NA		NA	NA

Note: Bold font type indicates lines with confidence interval excluding zero.

Abbreviations: CI, confidence interval; Imp., importance of the parameters within the model averaging; n, number of models taken into account for model averaging; NA, not applicable; SE, standard error.

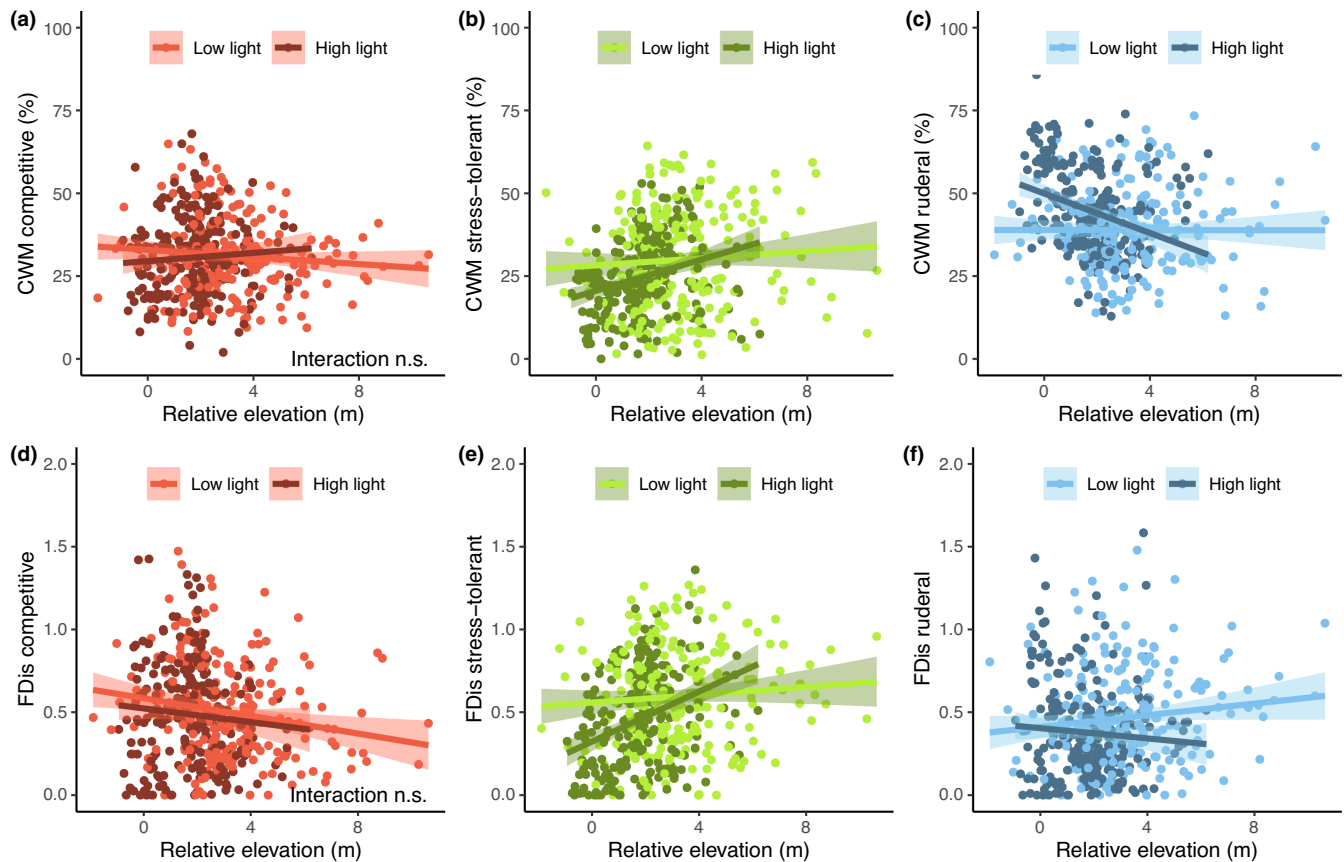


FIGURE 3 Response of community-weighted mean (CWM) and functional dispersion (FDis) values for competitive, stress-tolerant and ruderal strategies to the interaction between relative elevation and light availability. Low light, <50%; high light, >50%; n.s., non-significant. Sign and magnitude of effects are reported in [Tables 1](#) and [2](#) for CWM and FDis respectively.

3.4 | Effects of environmental gradients on the dispersion values of ecological strategies

Regarding functional dispersion ([Table 2](#)), values for competitors (C_{FDis}) were significantly influenced by the interaction between *grain size* and *elevation* ([Figure 5d](#)) as well as by the interaction between *grain size* and *slope* ([Figure 6d](#)), revealing a more pronounced decrease in C_{FDis} values at sites dominated by coarse sediment with increasing *elevation* and *slope*. For the dispersion values of stress tolerators (S_{FDis}), the interaction between *light* and *elevation* was significant, that is, in high light conditions S_{FDis} increased along the elevation gradient while in shady conditions S_{FDis} remained stable ([Figure 3e](#)). Finally, for the dispersion values of ruderals (R_{FDis}), *distance* had a significant positive effect and three interaction terms were significant ([Table 2](#)): *light* and *grain size*, that is, R_{FDis} values increased with light at locations dominated by coarse sediments but decreased at sites dominated by fine sediments ([Figure 7f](#)); *light* and *elevation*, that is, in high light conditions R_{FDis} decreased along the elevation gradient while in shady conditions it increased ([Figure 3f](#)); and *elevation* and *grain size*, that is, R_{FDis} values increased with elevation at sites dominated by fine sediments but decreased at locations dominated by coarse sediments ([Figure 5f](#)).

4 | DISCUSSION

4.1 | Response of taxonomic composition to environmental gradients

The results of this study highlight differences in species composition across each environmental gradient (i.e., elevation, slope and position along the side channel, light and sediment grain size). In riparian ecosystems, the link between elevation and water level—as a proxy for flood disturbance or water availability—and species assemblage is well established for both small streams and large rivers (Bornette et al., 2008; Marchetti & Aceñolaza, 2012; Garssen et al., 2017; McCoy-Sulentic et al., 2017). However, elevation is involved in both dispersal limitation (Fraaije, ter Braak, Verduyn, Verhoeven, & Soons, 2015; Pereira et al., 2021) and environmental filtering (Zelnik & Čarni, 2008; Janousek & Folger, 2014; Damgaard et al., 2017). Therefore, identifying which of these two processes dominates along the elevation gradient remains challenging. Moreover, the latter is likely to vary stochastically within the Loire river floodplain (Greulich et al., 2019; Gaudichet et al., 2022). Generally, side channel top banks were colonized by trees (either naturally or planted by humans), whose canopy filters incident light. Therefore, elevation and light were negatively correlated. Not surprisingly, light is the primary resource gradient shaping herbaceous

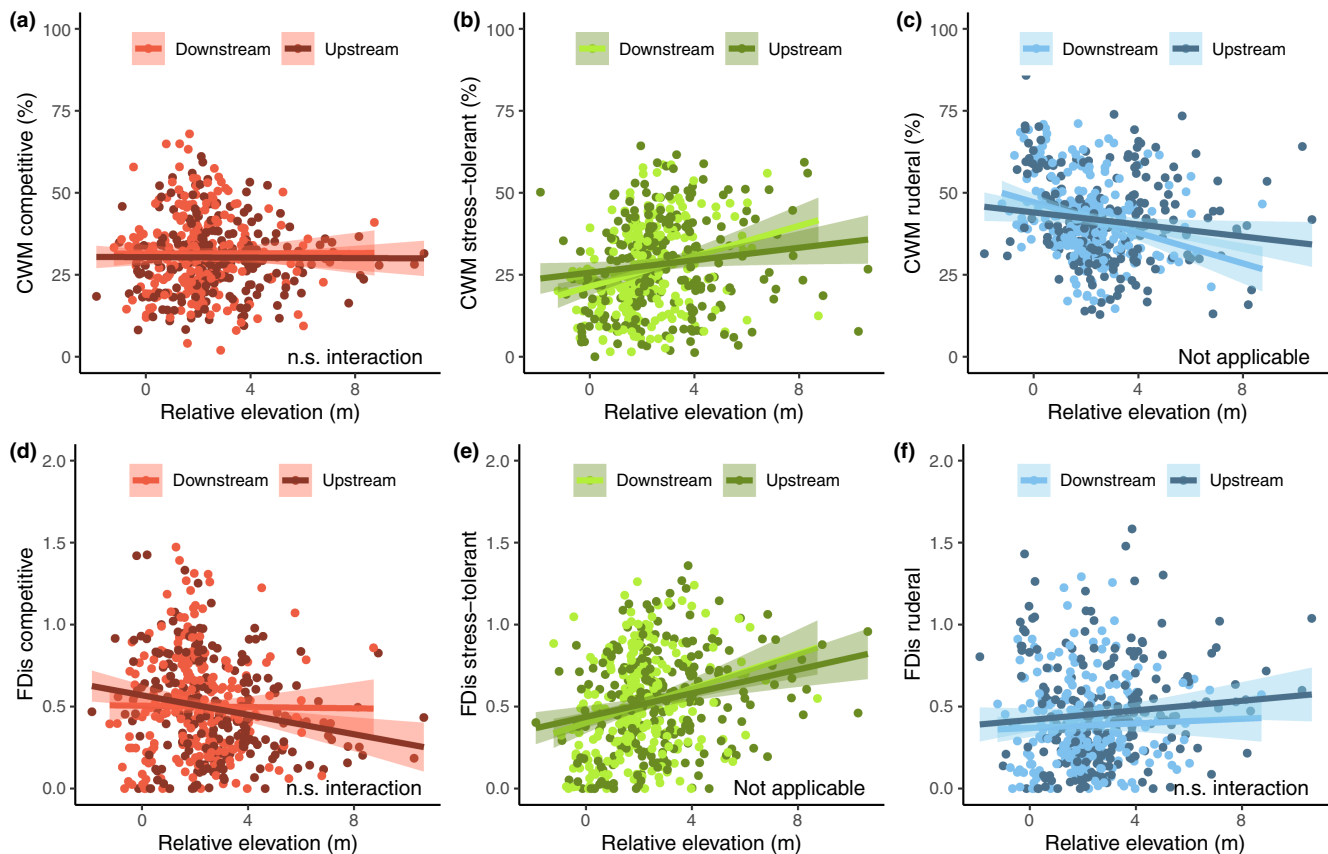


FIGURE 4 Response of community-weighted mean (CWM) and functional dispersion (FDis) values for competitive, stress-tolerant and ruderal strategies to the interaction between relative elevation and plot position within side channels. Low light, <50%; high light, >50%; n.s., non-significant. Sign and magnitude of effects are reported in Tables 1 and 2 for CWM and FDis respectively.

communities, as shown in other studies (e.g., Terwei et al., 2016). Secondly, sediment properties participate in environmental filtering when light is not a limiting resource. Thus, at the reach and side channel scales, substrate diversity should have a positive effect on species richness. Studies taking into account slope in riparian zones are rare. We found only one study on the Current and Jack Fork rivers (Missouri, USA), which showed an effect of slope on species composition (Lyon & Sagers, 1998). The results were similar to ours. To the best of our knowledge, the effect of position within side channels was poorly studied for terrestrial species, but there is evidence of its structuring effect as an environmental filter (Gaudichet et al., 2022).

Taxonomic composition responded significantly to all environmental parameters that we measured. The high proportion of unexplained inertia may be attributed to other community processes such as biotic interactions, seed bank formation as well as unmeasured environmental gradients (e.g., duration of hydrological phases, water salinity).

4.2 | Overall response of ecological strategies to environmental gradients

As sensed by fitting the mean and dispersion values of ecological strategies with species ordination (Figure 2a), both stress tolerator and ruderal mean values responded to (almost) the same environmental gradients, and they did it in an opposite manner. In addition,

the sets of environmental gradients affecting functional dispersion varied for each CSR strategy. As hypothesized (hypothesis 6 above), numerous environmental gradients interacted. It is therefore not possible to fully validate hypotheses 1, 2, 4 and 5. Main effects and interaction effects of environmental gradients on ecological strategies are discussed below, one by one. However, we can reject hypothesis 3 because no effect of environmental gradients was observed on the mean value of competitors within the communities. This result may be related to the absence or to the low frequency/abundance of competitive species (i.e., tall herbs and forbs, trees and shrubs) in the data set (Li & Shipley, 2017).

4.3 | Main effects of environmental gradients on ecological strategies of side channels communities

The main structuring effects on ecological strategies of plant communities were handled by two out of three topographical parameters. First, slope affected the balance between stress tolerator and ruderal mean values. Second, proximity to the upstream end of a side channel had a positive effect on the dispersion values of ruderal strategy.

With slope representing a local variation in elevation, one could expect that it may favor the co-occurrence of several strategies at a very short distance. This has been confirmed for the case of alpine ecosystems with regard to the leaf traits LDMC and SLA and an alternative

TABLE 2 Model averaging of functional dispersion (FDIs) for C (competitive), S (stress-tolerant) and R_s (ruderal) strategies.

Parameters	FDIs C		39		FDIs S		n =		19		FDIs R		n =		35	
	Imp.	n =	Estimate (±SE)	(95% CI)	Imp.	n =	Estimate (±SE)	(95% CI)	Imp.	n =	Estimate (±SE)	(95% CI)	Imp.	n =	Estimate (±SE)	(95% CI)
Tide	1.00	0.018 (±0.020)	(-0.022; 0.058)	1.00	0.014 (±0.024)	(-0.032; 0.060)	1.00	0.054 (±0.027)	(0.001; 0.107)							
Rainfall	1.00	0.029 (±0.019)	(-0.008; 0.065)	1.00	-0.002 (±0.022)	(-0.046; 0.042)	1.00	-0.057 (±0.026)	(-0.108; -0.006)							
Temperature	1.00	0.044 (±0.017)	(0.010; 0.077)	1.00	0.003 (±0.022)	(-0.041; 0.047)	1.00	0.036 (±0.027)	(-0.016; 0.088)							
Light	0.35	-0.022 (±0.017)	(-0.055; 0.011)	1.00	-0.040 (±0.017)	(-0.074; -0.007)	0.97	-0.044 (±0.014)	(-0.072; -0.016)							
Elevation	0.85	-0.031 (±0.017)	(-0.065; 0.002)	0.96	0.065 (±0.022)	(0.021; 0.109)	0.29	0.007 (±0.020)	(-0.032; 0.047)							
Grainsize	0.97	0.037 (±0.017)	(0.004; 0.071)	0.17	-0.010 (±0.017)	(-0.043; 0.024)	0.81	0.024 (±0.018)	(-0.011; 0.058)							
Distance	0.31	-0.017 (±0.014)	(-0.045; 0.011)	0.13	-0.005 (±0.014)	(-0.032; 0.022)	0.63	0.027 (±0.013)	(0.002; 0.052)							
Slope	0.26	0.007 (±0.015)	(-0.021; 0.036)	0.46	0.024 (±0.015)	(-0.005; 0.053)	0.22	0.019 (±0.014)	(-0.010; 0.047)							
Light * elevation	0.01	-0.003 (±0.017)	(-0.036; 0.030)	0.85	0.049 (±0.017)	(0.016; 0.082)	0.07	-0.034 (±0.016)	(-0.066; -0.002)							
Light * grain size	0.03	0.014 (±0.015)	(-0.016; 0.044)	0.02	0.028 (±0.015)	(-0.001; 0.057)	0.44	0.034 (±0.014)	(0.007; 0.062)							
Light * distance	0.00	0.007 (±0.014)	(-0.020; 0.034)	NA	NA	NA	0.06	-0.013 (±0.013)	(-0.038; 0.011)							
Light * slope	NA	NA	NA	0.02	0.012 (±0.014)	(-0.016; 0.040)	0.01	-0.008 (±0.013)	(-0.034; 0.019)							
Elevation * grain size	0.51	-0.034 (±0.015)	(-0.063; -0.004)	0.00	-0.022 (±0.015)	(-0.052; 0.007)	0.11	-0.040 (±0.015)	(-0.068; -0.011)							
Elevation * distance	0.04	-0.022 (±0.014)	(-0.049; 0.006)	NA	NA	NA	0.01	0.020 (±0.013)	(-0.005; 0.045)							
Elevation * slope	0.01	-0.013 (±0.014)	(-0.039; 0.014)	0.02	-0.012 (±0.013)	(-0.038; 0.014)	NA	NA	NA							
Grainsize * distance	0.02	0.005 (±0.015)	(-0.024; 0.035)	NA	NA	NA	0.09	0.026 (±0.014)	(-0.001; 0.053)							
Grainsize * slope	0.11	-0.031 (±0.014)	(-0.059; -0.002)	NA	NA	NA	0.01	-0.017 (±0.013)	(-0.043; 0.009)							
Distance * slope	NA	NA	NA	NA	NA	NA	0.02	-0.019 (±0.012)	(-0.043; 0.006)							

Note: Bold font type indicates lines with confidence interval excluding zero.

Abbreviations: CI, confidence interval; Imp., importance of the parameters within the model averaging; n, number of models taken into account for model averaging; NA, not applicable; SE, standard error.

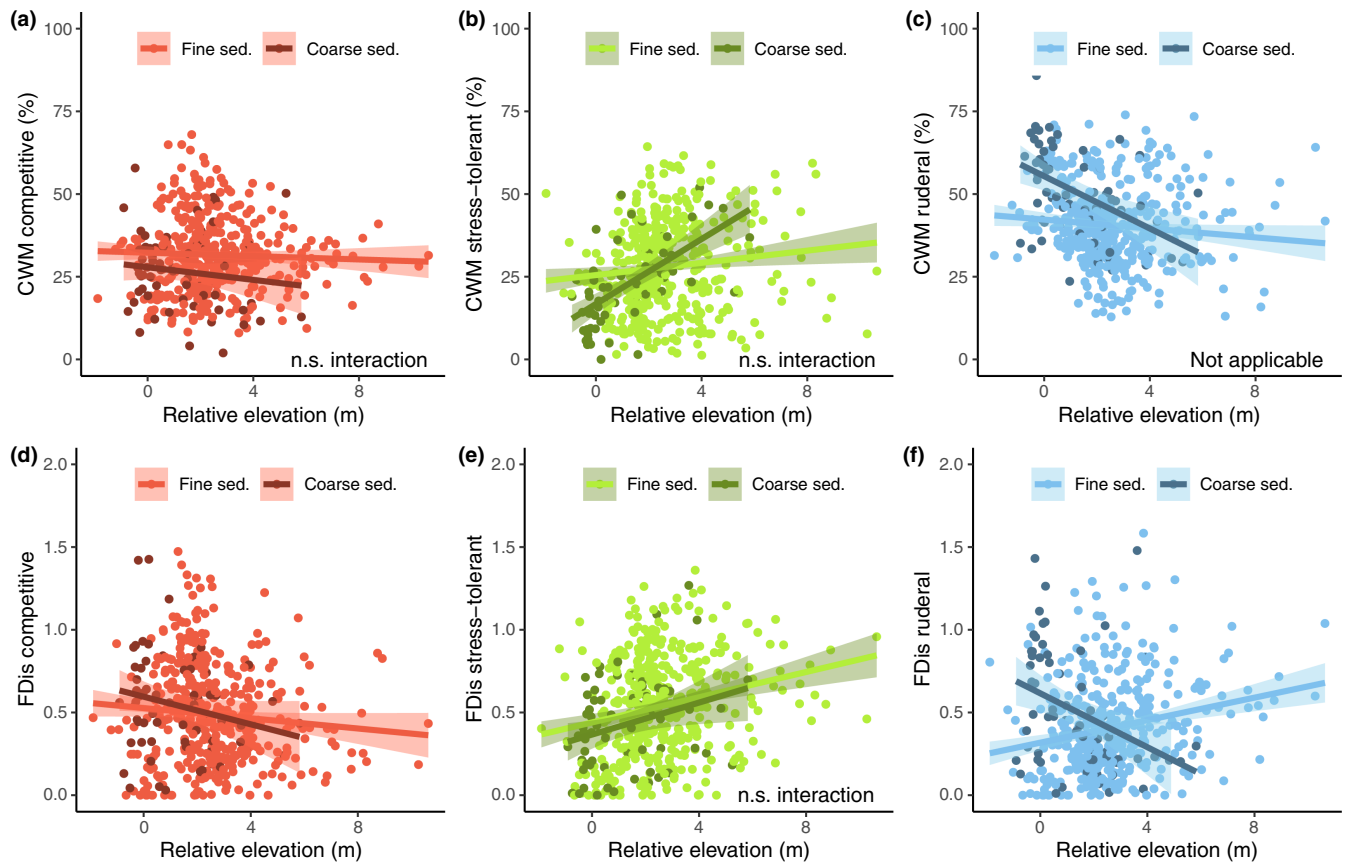


FIGURE 5 Response of community-weighted mean (CWM) and functional dispersion (FDis) values for competitive, stress-tolerant and ruderal strategies to the interaction between relative elevation and sediment grain size. Fine sed., fine sediment (≤ 2 mm); coarse sed., coarse sediment (> 2 mm); n.s., non-significant. Sign and magnitude of effects are reported in [Tables 1](#) and [2](#) for CWM and FDis respectively.

index of community functional range (de Bello et al., 2013). Surprisingly, our results showed that slope favors stress tolerator over ruderal strategy. One possible explanation is that the upper sediment layer may experience run-off. As a consequence, small-seeded species (i.e., typically R strategists; Bornette et al., 2008; Grime, 1977) may be washed away to the benefit of perennial and geophyte species with better anchorage (Mallik et al., 2001; Bochet, 2015). Thus, the plot inclination would act as a dispersal filter preventing propagule arrival, rather than an environmental filter in the strict sense (Kraft et al., 2015). At the channel scale, our result is consistent with those of Fraaije et al. (2019), who studied the effect of channel restoration (meandering and widening) on riparian vegetation: ruderal mean values were associated with restored wide channels (gentle bank slope), and perennials and stress tolerators were associated with unrestored confined channel (steep bank slope).

We found a positive effect of the downstream-upstream gradient on the range of ruderal scores. However, the fact that the mean ruderal value did not vary along the downstream-upstream gradient indicates that variations of the disturbance level occur mostly across channels. Flood disturbance is thus likely to be similar at the downstream end of the side channels, while a variety of flooding conditions occur at the upstream end of side channels. Overall, and depending on the exposure of the upstream part of the side channels to flooding, this allows the co-occurrence of a wider range of ruderal values, from species highly adapted to disturbance to species more suited to stable environments.

4.4 | Interaction effects of environmental gradients on ecological strategies of side channel communities

As expected, interaction effects between environmental gradients structured community CSR strategies. Especially elevation, light and sediment grain size were identified to be the most important drivers of changes in the ecological strategies of plant communities of side channels.

4.4.1 | Light deprivation induces a homogenization of ecological strategies along the elevation gradient

The interaction between light and elevation influenced significantly the mean and dispersion values of stress-tolerators and ruderals (i.e., CWM and FDis). In case of low light availability, stress tolerators and ruderals remained rather stable along the elevation gradient, whereas in case of high light availability, there was a switch between stress tolerators, which increased with elevation, and ruderals, which decreased with elevation. Canopy closure over the side channel was detrimental for ruderal strategy along the talweg of side channels, but it mitigated the dominance of stress-tolerant strategies on banks. Thus, species' ecological strategies within communities tend

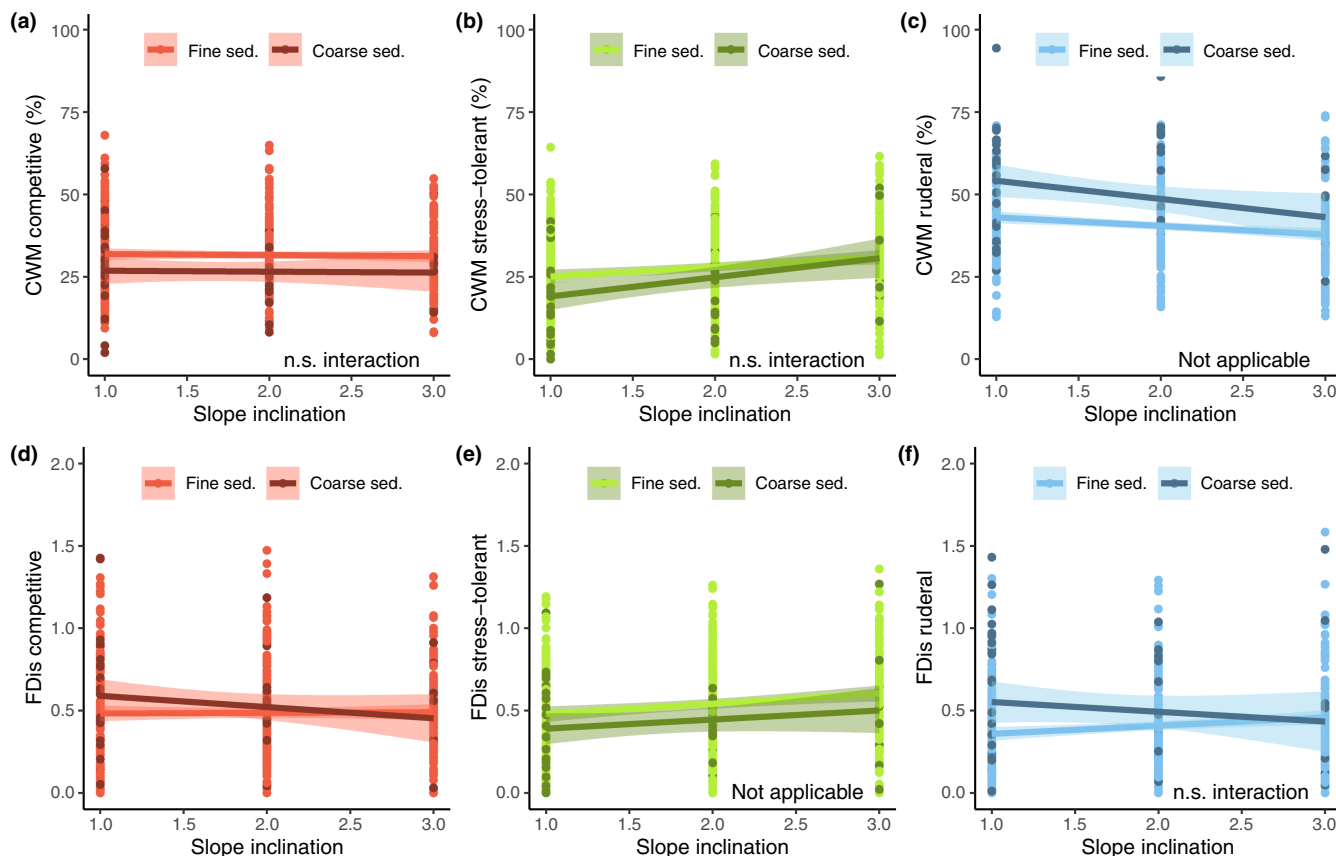


FIGURE 6 Response of community-weighted mean (CWM) and functional dispersion (FDis) values for competitive, stress-tolerant and ruderal strategies to the interaction between slope and sediment grain size. Slope 1, inferior to 5°; 2, comprised between 5° and 30°; 3, comprised between 30° and 70°. Coarse sed., coarse sediment (>2 mm); fine sed., fine sediment (≤2 mm); n.s., non-significant. Sign and magnitude of effects are reported in [Tables 1](#) and [2](#) for CWM and FDis respectively.

to homogenize across the flooding gradient in case of canopy closure, to the favor of shade-tolerant species. This is consistent with Grime's theory (1977) and field experiments in wet grassland communities (Xiong et al., 2003) or mesocosm experiments on wetland species (Kotowski et al., 2010) that tested for interacting effects between canopy presence and other stress/disturbance gradients. Xiong et al. (2003) showed that the vshaded condition is the strongest filter for seedling recruitment (i.e., low functional and taxonomic diversity), despite variations in soil moisture, nutrient availability or mowing. However, in some cases, such as found in arid non-riparian ecosystems, shading mitigates stress tolerance to drought independently of the disturbance gradient (Escobedo et al., 2021).

4.4.2 | Longitudinal position within side channels affects stress-tolerant strategies along the flooding gradient

Finding interacting effects between elevation and longitudinal position in the side channel on the mean value of stress tolerators within communities was unexpected. Indeed, we hypothesized that both gradients would affect the ruderal strategy instead. At

the downstream end, partitioning of resources seemed to occur along the elevation gradient. Mechanisms sustaining this interaction effect remain unclear. One possible explanation is that the downstream end is generally more protected from turbulent flows than the upstream end (Rodrigues et al., 2006; van Denderen et al., 2019). Thus, the downstream end would be prone to sedimentation and nutrient accumulation at the talweg, while nutrient redistribution should occur along the elevation gradient at the upstream end. Possibly, other parameters such as differences in flooding conditions (i.e., duration, magnitude, intensity), or water physicochemical properties, which affect seedling recruitment, may be confused with elevation and distance gradients (e.g., Bornette, 1991; Fraaije, ter Braak, Verduyn, Breeman, et al., 2015).

4.4.3 | Silting reduces the co-occurrence of plant species with different ecological strategies within communities

Sediment grain size significantly influenced the dispersion values related to competitive and ruderal strategies within communities. Sediment fining lowered the range of competitor scores on plots

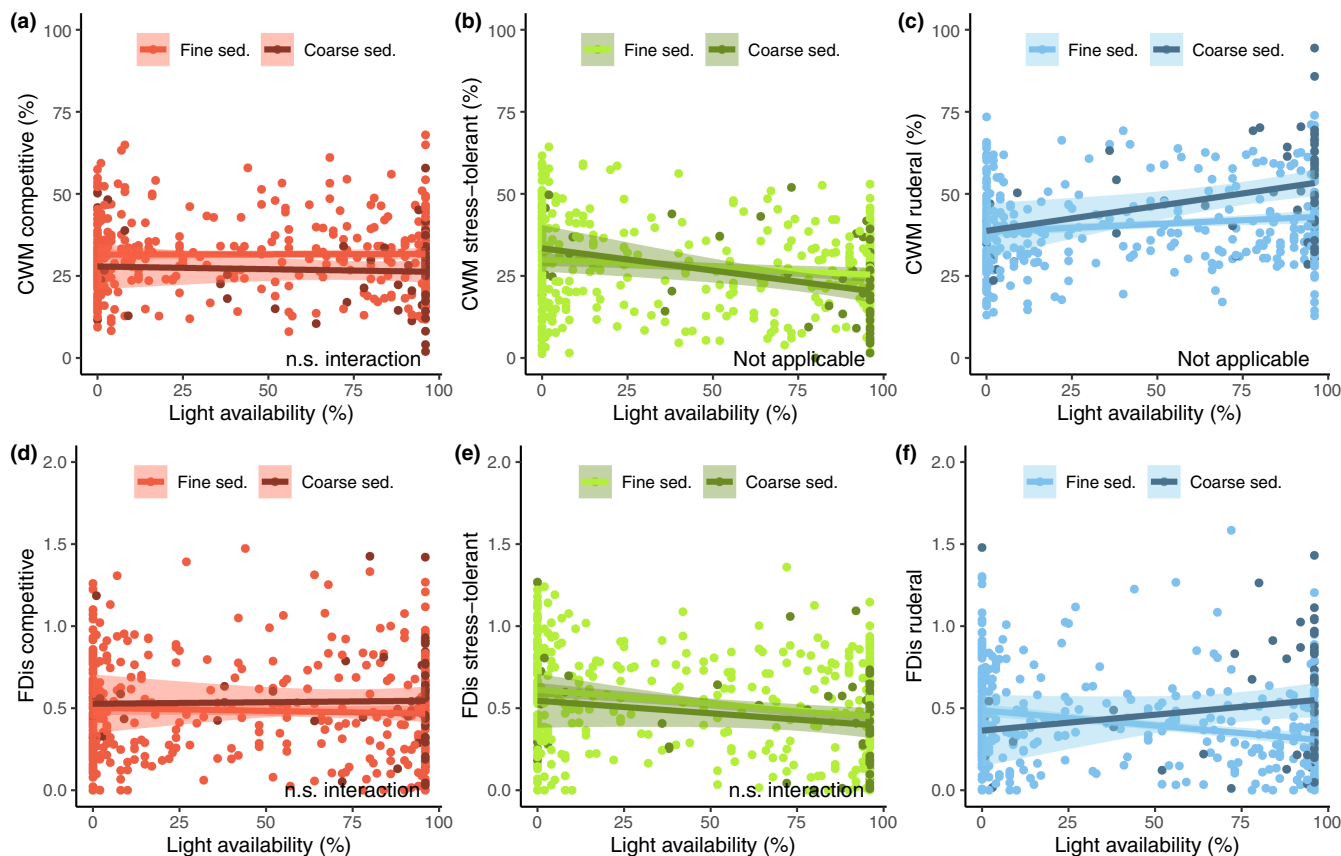


FIGURE 7 Response of community-weighted mean (CWM) and functional dispersion (FDis) values for competitive, stress-tolerant and ruderal strategies to the interaction between light availability and sediment grain size. Coarse sed., coarse sediment (>2 mm); fine sed., fine sediment (≤ 2 mm); n.s., non-significant. Sign and magnitude of effects are reported in [Tables 1](#) and [2](#) for CWM and FDis respectively.

with low elevation or gentle slope and it lowered the range of ruderal scores in the case of high light availability and low elevation (i.e., pioneer environmental conditions). Thus, it appears that sediment grain size is more likely to indicate the level of disturbance rather than the availability of nutrients and water at low elevation. Indeed, sediment characteristics depend on deposition conditions such as flow velocity, channel morphology, water surface slope and bed roughness (Nicholas & Walling, 1998; Steiger & Gurnell, 2003; Claude et al., 2012). The combination of environmental conditions that are typical of alluvial bars (i.e., high light availability, low elevation and gentle slope) were found to have similar effects on the vegetation strategies on the Rhône river (Janssen et al., 2020), and substrate clogging was identified as a threat for typical ruderal communities in other hydrosystems (Piégay et al., 2000; Asaeda & Sanjaya, 2017). As an illustration in our study, the alien plant species in the *Ludwigia* genus were highly associated with fine sediments at low elevation levels. In the context of fluvial biogeomorphologic succession (Corenblit et al., 2009; Tabacchi et al., 2019; Corenblit et al., 2020), smaller grain size and decline in disturbance level indicate a shift from a biogeomorphic phase (i.e., an ecosystem shaped by reciprocal interactions between abiotic and biotic drivers) to an ecological phase (i.e., an ecosystem dominated by biotic interactions).

5 | CONCLUSION

One original approach of this study lies in the acquisition of a large data set on the distribution of terrestrial species in riverine side channels. Our results demonstrate that local environmental gradients related to light, sediment grain size and hydrological connectivity have significant and non-independent influences on the taxonomic composition and ecological strategies of plant communities in riverine side channels. We showed that gradients of stress (illustrated by light and sediment grain size) and disturbance (illustrated by elevation and distance from the downstream end of side channels) strongly shaped community composition. Using information contained in leaf traits to derive species' ecological strategies allowed us to reveal complex interactions between these two gradients. Thus, light availability mitigated the structuring effect of the topographic gradient for stress-tolerant and ruderal dimensions of the communities, that is, on shaded banks along the channel cross-section, environmental selection of species was less strong than under full light conditions. Furthermore, we demonstrated that shaded conditions and fine sediments favor plant communities with less differentiated ecological strategies along the elevation gradient, suggesting a strong effect of these parameters on species niche homogenization. Overall, our results show that stress and disturbance gradients interact at fine spatial scales and sometimes in complex ways

to shape herbaceous communities in side channels. Restoration of side channels should target a wide range of light and sediment grain size conditions to allow the expression of taxonomic and functionally rich plant communities.

AUTHOR CONTRIBUTIONS

C. Gaudichet conceived the research idea and collected the data; C. Gaudichet and P. Janssen performed the statistical analysis; C. Gaudichet, with contributions from P. Janssen, Séraphine Grellier and Sabine Greulich, wrote the paper; all authors discussed the results and commented on the manuscript.

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DATA AVAILABILITY STATEMENT

Data are available in supporting information (Appendix S7). Traits data were extracted from the TRY database (requests: 15018, 15049, 15445).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Characteristics of study sites.

Appendix S2. Location and aerial photographs of study sites.

Appendix S3. Species list and CSR scores.

Appendix S4. Model forms.

Appendix S5. Correlogram of environmental parameters.

Appendix S6. Top-ranked models.

Appendix S7. Data.

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