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## SPECIES COMPOSITION AND PLANT TRAITS: CHARACTERIZATION OF THE BIOGEOMORPHOLOGICAL SUCCESSION WITHIN CONTRASTING RIVER CORRIDORS

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### Abstract

Plant communities and dynamics can be characterized according to species composition or plant traits. Here, we used species composition and plant traits to compare their effectiveness in discriminating the biogeomorphological (involving reciprocal feedbacks between physical and biological processes) and ecological (mainly biologically driven) phases of the fluvial biogeomorphological succession (FBS) model. The comparison was done between two French rivers, the largely unchannelized lower Allier and the channelized middle Garonne. One reach representative of each river section was selected for the study. Within each river reach, we chose two contrasted study sites in terms of channel and floodplain dynamics: a reference site (least altered channel and floodplain dynamics) and an altered site (laterally stabilized by riprap and constrained). In the four study sites, we sampled vegetation in 402 plots of 4 m<sup>2</sup>. The 512 species identified in the plots were characterized in terms of plant traits (20) from a literature review. When comparing reaches in unconstrained ordinations and permutational multivariate analyses of variance, both species composition and plant traits led to a similar identification of the biogeomorphological and the ecological successional trajectories. Nevertheless, the trait approach was less influenced by local and regional bioclimatic, hydrogeomorphological, and anthropogenic settings and thus produced a more comprehensive and general classification of the biogeomorphological and ecological phases of the FBS model. A lower than expected contrast between the four sites was found, because neither species composition nor plant traits could entirely characterize distinct successional trajectories occurring in our reference or altered sites. Furthermore, our results contributed to a better understanding of the multiple successional trajectories that can occur in midlatitude river corridors. It also showed that relating plant traits to their effects on fluvial landform dynamics remains a core challenge in explaining succession including feedback mechanisms between hydrology, morphodynamics, and vegetation dynamics.

### Keywords

Allier River, channelized, fluvial biogeomorphological succession, Garonne River, plant traits, riparian vegetation, species composition, unchannelized.

## 1 Introduction

The original concept of ecological succession (Clements, 1916) described species replacement following progressive changes in the relationships between organisms and their natural environment. Clements' original concept of a unique deterministic successional trajectory drastically evolved during the 1980s with physical disturbances or stress being identified as the main or secondary drivers of change (Connell & Slatyer, 1977; Pickett, Kolasa, Armesto, & Collins, 1989; Tilman, 1990; Walker & Chapin, 1987). It was suggested that local changes in the environment can induce bifurcations in succession trajectories, and this led to a theoretical multiple pathway framework of succession (Cattalino, Noble, Slatyer, & Kessell, 1979; Cooper, Andersen, & Chimner, 2003). Along environmental gradients, for example, generated by topography, moisture, nutrients, or exposure to disturbance, autogenic and allogenic drivers may sequentially interact and produce distinct successional trajectories including regressions. This is the case of riparian and floodplain areas within river corridors (Bridge, 2003; Naiman, Décamps, & McClain, 2005; Shull, 1922) where both fluvial landforms and vegetation are exposed to important variations in hydrosedimentary dynamics, resulting in specific plant strategies operating at different spatiotemporal gradients and scales (Johnson, 1994; Hupp & Osterkamp, 1996; Bornette, Tabacchi, Hupp, Puijalon, & Rostan, 2008).

Several authors (Corenblit, Steiger, Gurnell, Tabacchi, & Roques, 2009; Corenblit, Tabacchi, Steiger, & Gurnell, 2007; Gurnell et al., 2016; Hupp, Osterkamp, & Howard, 1995; Naylor, Viles, & Carter, 2002) have identified successional phases, which involve a reciprocal coupling between hydrogeomorphological and ecological processes for explaining the synchronized changes in fluvial landforms and vegetation observed in the field over time. The fluvial biogeomorphological succession concept (FBS model hereafter; Corenblit et al., 2007) pointed out that these synchronized changes include (a) the initial response of vegetation to the hydrogeomorphological conditions and processes, (b) the effect of engineer (sensu Jones et al., 1994) plants on hydrogeomorphological processes, and (c) the response of vegetation to the biologically controlled changes of the habitat conditions. A specificity of the biogeomorphological succession concept is that engineer plant species potentially play an important role as both response and effect agents (Corenblit, Steiger, Tabacchi, González, & Planty-Tabacchi, 2014). The FBS model distinguishes four successional phases:

- (i) a geomorphological phase where river flow and floods, that is, hydrogeomorphological disturbance, create and maintain fluvial landforms composed of bare sediment. At this stage, hydrogeomorphological processes define the settings for plant dispersal and recruitment;
- (ii) a pioneer phase where new plants recruit. At this stage, hydrogeomorphological conditions and processes exert a prominent one-way control on vegetation dynamics;
- (iii) a biogeomorphological phase where established engineer plants control both landform construction and plant community dynamics; and
- (iv) an ecological phase where the exposure of vegetation to hydrogeomorphological disturbance becomes negligible and biotic interactions dominate succession.

The distinction between the biogeomorphological (phase iii) and the ecological (phase iv) phases of the FBS model is sometimes difficult because of very subtle spatiotemporal variations in the type and intensity of interactions between physical and biological drivers. Such variations, for example, related to channel migration, vertical incision, changes in flood regime, or biotic activities (e.g., grazing), can affect the trajectory of succession while being hardly detectable on a short timeline.

Classically, a floristic approach has been used to describe changes in vegetation during succession (Amoros & Wade, 1996). Such an approach is very sensitive to local (habitat) and regional (biogeography) settings and may limit the power of generalization among river systems with different characteristics. Furthermore, species taxonomy does not directly address the underlying mechanisms coupling physical and biological processes. An alternative is to consider plant (functional) traits instead, or in addition to, species composition. During the past two decades, the trait-based approach has been increasingly and successfully used in community ecology (Diaz, Cabido, & Casanoves, 1998; McGill, Enquist, Weiher, & Westoby, 2006). It is less affected by local variability and may facilitate generalization among systems (Shipley et al., 2016).

In the riparian context, the trait-based approach has been applied to study functional changes in terms of vegetation response and effects along environmental gradients (Aguar et al., 2018; Merritt, Scott, LeRoy Poff, Auble, & Lytle, 2010; Stromberg & Merritt, 2016). As suggested by Corenblit et al. (2015), the trait approach, more representative of biogeomorphological interactions and feedbacks from a functional point of view than the classic taxonomic approach, is the best solution to discriminate between phases of the FBS model. The authors stated that rivers across the world exhibit a huge taxonomical variability, but equivalent environmental constraints apparently led to convergent patterns of adaptive traits across taxa. For example, pioneer riparian plant species present similar morphological, biomechanical, and life history attributes optimizing their recruitment and establishment. The power of the trait-based approach to relate vegetation to hydrogeomorphological dynamics within a biogeomorphological perspective has been demonstrated. For example, O'Hare, Mountford, Maroto, and Gunn (2016) used large datasets of traits more or less directly related to the effect of plants on hydrogeomorphology and fluvial landforms modulation, whereas Diehl, Merritt, Wilcox, and Scott (2017) provided an eco-geomorphic modelling approach calibrated with in situ measurements, which established links between engineer plant response and effect traits. Because the effect of vegetation on fluvial geomorphology is correlated to its response traits, the trait approach appears to be efficient for describing biogeomorphological feedbacks driving the FBS. However, to our concern, no study has explicitly compared the capacity of the taxonomic and functional approaches to discriminate phases of the FBS model.

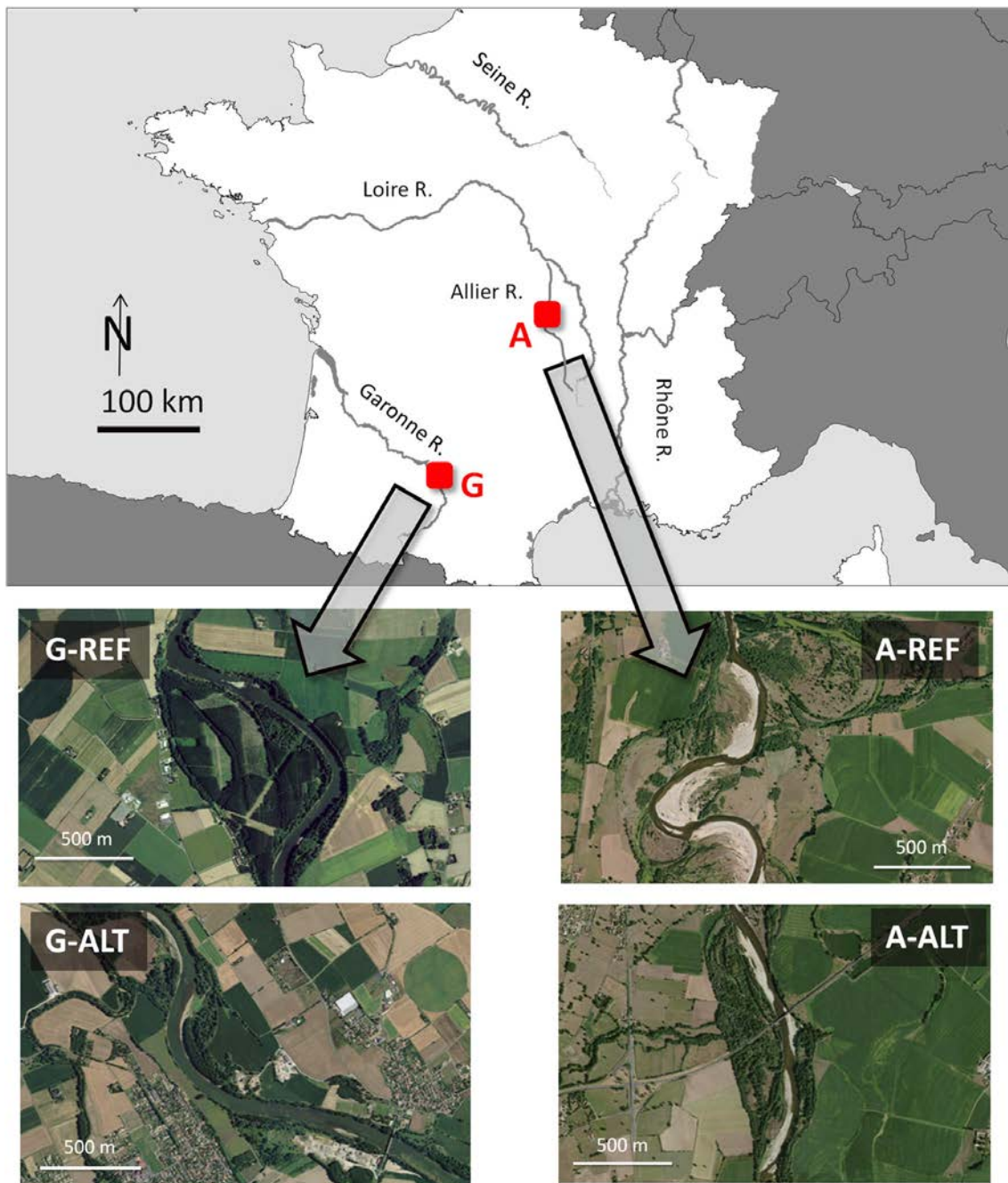
In this article, we investigated the complementarity of the taxonomic species composition and the trait-based approach (a) to characterize the last two phases of the FBS model (i.e., the biogeomorphological [iii] and the ecological [iv] phases), which are the least easily distinguishable, and (b) to identify plant succession related to successional trajectories within the FBS model. To test the repercussion of our study across different rivers, we selected two river reaches with a different degree of human alteration by channelization, that is, the modification of the river and its channel, for example, for bank erosion reduction or flood risk prevention. Furthermore, within each river reach, we compared two contrasted sites, a reference site (least altered channel and floodplain dynamics) and an altered site (laterally stabilized by riprap and constrained).

## 2 Materials and methods

### 2.1 Study sites

We studied two French river reaches: the lower Allier River and the middle Garonne River (**Figure 1**). The hydrological regime of the Allier is pluvial (Onde, 1923), whereas the regime of the Garonne river is pluvio-nival (Pardé, 1935). In contrast to the laterally unconstrained, unchannelized lower Allier River (Garófano-Gómez et al., 2017), the middle Garonne River was heavily impacted by river bank protections (riprap), sediment mining, and upstream dam construction during the second half of the 20th century, leading to channelization and vertical incision of the river channel (Jantzi, Carozza, Probst, & Valette, 2017; Steiger, James, & Gazelle, 1998).

Within each of these two river reaches, we selected two contrasted study sites (**Figure 1**): one reference site with no or few river training works, that is, least altered channel and floodplain dynamics within each reach (A-REF, local name: Châtel de Neuvre, 46.416°N, 3.231°E, 219 m a.s.l.; G-REF, local name: Verdun-sur-Garonne, 43.833°N, 1.250°E, 99 m a.s.l.), and one characterized by river training works and human-induced lateral stability (A-ALT, local name: Chemilly, 46.479°N, 3.328°E, 222 m a.s.l.; G-ALT, local name: Ondes-sur-Garonne, 43.752°N, 1.388°E, 118 m a.s.l.). The contrast between G-REF and G-ALT of the Garonne River was much lower than between A-REF and A-ALT of the Allier River, because the reference site G-REF only represented the least impacted conditions within an overall highly modified reach (Tabacchi & Planty-Tabacchi, 2005).



**Figure 1.** Location of the study river reaches in the contrasted French middle Garonne (G) and lower Allier (A) rivers (top, red squares). Aerial photographs (2012) of the reference sites (A-REF and G-REF) and the channelized sites (A-ALT and G-ALT; bottom). Photos were obtained from the Institut Géographique National of France.

Although the riparian vegetation of the Allier River remains relatively well preserved from human influence (Garófano-Gómez et al., 2017), that of the Garonne River is now reduced to a few remnant patches that established next to poplar plantations (González, Masip, & Tabacchi, 2016; Muller, Guilloy-Froget, Barsoum, & Brocheton, 2002). Where poplar plantations are absent, the floodplain is mainly occupied by field crops and orchards. Atlantic riparian vegetation, mainly dominated by black poplar (*Populus nigra*) and white willow (*Salix alba*) forests at pioneer and postpioneer stages, is present in both river systems. The canopy, in persistently wet and fine-grained habitats, mainly cut-off channel margins, is dominated by alder (*Alnus glutinosa*), fragile willow (*Salix fragilis*), and grey willow (*Salix atrocinerea*) on the Garonne River. Wet mature stages mainly consist of black poplar and Mediterranean ash (*Fraxinus angustifolia*) formations, or, in degraded, more heavily channelized river segments, to common elm (*Ulmus minor*) ruderal forests. The Garonne River no longer develops oak (*Quercus pubescens* or *Quercus robur*) mature forests. Along the Allier River, postpioneer mixed forests composed by short-lived riparian (*P. nigra*–*S. alba*) and terrestrial

(*Q. robur*–*Ulmus* sp.–*Robinia pseudoacacia*) tree species develop outside of the active tract channel in transition to the hardwood forest (Garófano-Gómez et al., 2017).

## 2.2 Successional phases

We will refer to phase (iii) of the FBS model as the B, that is, “biogeomorphological” successional phase from hereafter. According to the FBS model, plant communities in the B phase are mainly dominated by pioneer herbaceous and ligneous species able to withstand flooding (resistant strategy) and to colonize frequently flood-disturbed areas (resilient strategy). Such communities potentially trap and stabilize sediment of different texture with different intensity along the successional gradient. Changes in plant succession at this stage are more or less reversible according to the degree of connection with the hydrogeomorphological disturbance. The second successional phase of the FBS model considered in this study is the successional phase (iv) and will be referred to as the “ecological” or E phase from hereafter. The E phase is dominated by biotic interactions such as facilitation, tolerance, interspecific competition, or herbivory, because it occurs on more elevated, less frequently flooded areas and plant communities that mainly consist of competitive species. In general, only exceptional, high magnitude floods may reverse this phase.

## 2.3 Vegetation survey and classification

For the vegetation survey, 402 plots of  $2 \times 2$  m were located within the four study sites, with a total of 182 plots on the Allier River and 220 on the Garonne River (**Table S1**). Within each plot, the relative cover (%) of all individual species was estimated visually in July 2012. To represent a full gradient of habitat characteristics within the B and E succession phases, we first distinguished 11 vegetation/habitat classes (**Table 1**), derived from Corenblit et al. (2009), before reducing to nine classes for statistical analyses. The 402 plots were set-up to represent a balanced number of the 11 vegetation/habitat classes. Their detailed characterization, as well as the successional (B or E) phase that was assigned to each of the classes, is provided in **Table 1**.

**Table 1.** Typology of the vegetation types and habitat characteristics along the fluvial biogeomorphological succession model (nomenclature follows Corenblit et al., 2009).

Successional phase	Vegetation/habitat class	Type of vegetation and habitat characteristics
Geomorphological	G0	Bare sediment or with only very scarce vegetation within the bankfull channel or active tract of multithread channels
Biogeomorphological	B1	Scarce pioneer vegetation on the very frequently flooded alluvial bars within the bankfull channel or active tract of multithread channels
Biogeomorphological	B2	Dense herbaceous vegetation on the frequently flooded alluvial bars of the bankfull channel or active tract of multithread channels, as well as within side channels
Biogeomorphological	B3	Tree seedlings/saplings and scarce pioneer vegetation on the frequently flooded alluvial bars of the bankfull channel or active tract of multithread channels
Biogeomorphological	B4	Tall herbs, pioneer forests, and shrublands within the less frequently flooded areas of the bankfull channel and its margins
Biogeomorphological	B0	Cut-off channels and standing waterbodies with aquatic and amphibiotic vegetation
Ecological	E1	Low (scarce) vegetation on the upper bank and channel margins
Ecological	E2	Meadows and dense herbaceous vegetation on the upper bank and channel margins
Ecological	E3	Shrublands, early forested stages on the upper bank, and channel margins
Ecological	E4	Mature forest in the upper and lower banks and channel margins
Ecological	H0	Man-built or directly influenced habitats within the very infrequently flooded areas

*Note.* Classes G0 and B1, as well as E2 and H0, were pooled, for a total of nine vegetation/habitat classes to be finally analysed.

## 2.4 Species composition and plant trait analyses

We identified a total of 512 plant species within the 402 plots. Alpha diversity corresponded to species richness per  $2 \times 2$  m plot (surface area:  $4 \text{ m}^2$ ). Beta diversity was estimated from Bray–Curtis dissimilarity. Due to unequal number of plots sampled per vegetation and habitat class (see **Table 1** and **Table S1**), gamma diversity was standardized using the Mao Tau estimator (Colwell et al., 2012). Taxonomic nomenclature followed the Angiosperm Phylogeny Group (2016) IV nomenclature.

The initial choice of traits was based on information extracted from the Ellenberg et al. (1992), *Baseflor* database (Julve, 2016), *Flora Indicativa* (Landolt et al., 2010, rev. 2010), *Flora Gallica* (Tison & de Foucault, 2014), and Grime (2001). We used additional expert-based knowledge (E. Tabacchi) to correct missing information and to provide new qualitative information (e.g., concerning flexibility or plant architecture). Traits used here were theoretical, that is, not measured, and refer to adult individuals. This trait dataset approximately matches the traits used by O’Hare et al. (2016) and Diehl et al. (2017) for testing the FBS model. Unavailable traits, such as specific leaf area or seed mass (Westoby, 1998), could not be included.

Initially, 26 relevant traits were documented for the 512 species. Eleven traits were continuous or ordinal and 14 were categorical, for a total of 283 initial trait modalities (**Table S2**). Binary trait values were weighted (community weighted) or weighted and averaged (community weighted mean) by the cumulative relative abundances (Ackerly & Cornwell, 2007; Violle et al., 2007). After the exploration of trait multicollinearity using Spearman correlations, the trait set was subsequently reduced to 20 traits including 78 modalities.

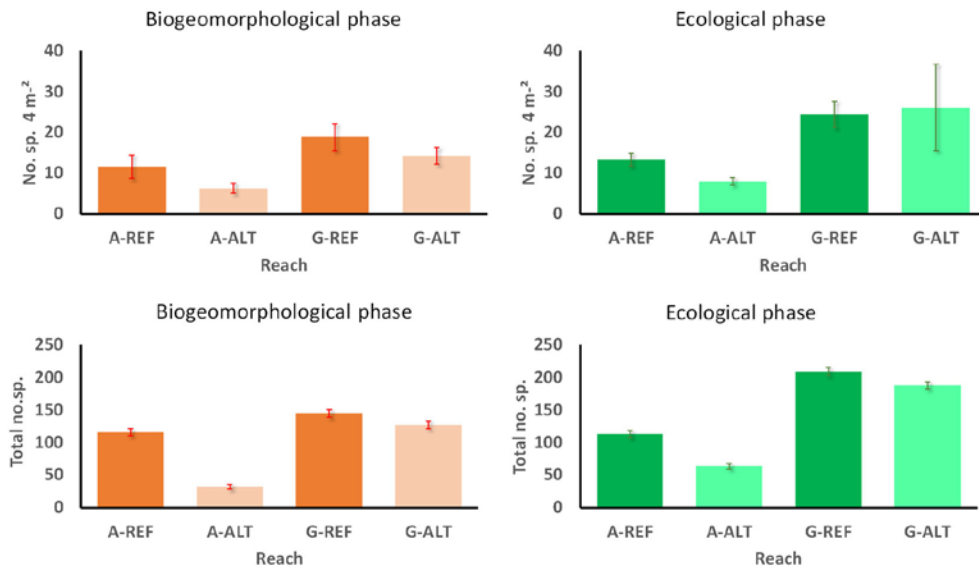
We conducted correspondence analysis (CA) on species relative abundance and principal component analysis (PCA) on trait characteristics. We used the site and species scores of the two ordinations along the two main gradients of variability to compare the effectiveness of the two approaches in separating the distinct sampling units: river reach, study site, FBS successional phase, and vegetation and habitat class. CA and PCA were processed using XLStat (v. 19.3, XLStat, 2018). The vegetation data were detrended prior to running the CA using Hellinger’s distances, because we used standardized relative cover to describe the species. Permutational multivariate analysis of variance (PERMANOVA) analyses, based on Bray–Curtis dissimilarity, were conducted to compare the entire plant community using a single factor (i.e., river reach, study site, or vegetation/habitat class) or type III interaction models (i.e., study site–vegetation/habitat class and river reach–vegetation/habitat class) under Monte Carlo bootstrapping. PERMANOVA analyses were processed with Primer-e v. 6.0 (Anderson, Gorley, & Clarke, 2015).

## 3 Results

### 3.1 Floristic composition

The floras of the Allier and Garonne river reaches differed (beta diversity–mean pairwise Bray–Curtis similarity of 37%, PERMANOVA,  $p < .001$ ). The five most abundant species found along the two rivers were *P. nigra*, *Urtica dioica*, *S. alba*, *Arrhenatherum elatius*, and *Phalaris arundinacea*. Along the Allier River, *P. nigra* was more abundant within the E phase, whereas along the Garonne River, it was more abundant within the B phase. Within the 10 most abundant species, three (*Tripleurospermum inodorum*, *Elytrigia × intermedia*, and *Berteroa incana*) were only found along the Allier River. Only one species (*Rubus ulmifolius*) was exclusive to the Garonne River.

The channelized middle Garonne was richer in species than the unchannelized lower Allier, in both the B and E phases (Mao Tau estimator, **Figure 2**). With the exception of the reference site of the Allier River (A-REF), the E phase showed higher gamma diversity (**Figure 2**) than the B phase. The laterally stabilized and altered site in the lower Allier (A-ALT) showed the lowest gamma diversity. Similar conclusions can be drawn for alpha diversity (**Figure 2**). The total mean species richness was  $15.3 \pm 0.6$  species per  $4 \text{ m}^2$ , with a maximum value of 74 species per plot. Differences among sites were significant (ANOVA,  $p < .001$ ) but not between G-REF and G-ALT.



**Figure 2.** Alpha (top) and gamma (bottom) species diversities observed in the four study sites according to plots assigned to the biogeomorphological (orange) and ecological (green) successional phases. Gamma diversity was standardized using Mao Tau estimator ( $n = 18$ ).

Species	Garonne River		Allier River	
	Biogeomorphological	Ecological	Biogeomorphological	Ecological
<i>Impatiens glandulifera</i> *	0.283	2.798	0.000	0.000
<i>Buddleja davidii</i> *	0.028	2.856	0.000	0.000
<i>Rubus gr. ulmifolius</i>	0.028	10.142	0.000	0.000
<i>Elytrigia repens</i>	0.341	5.703	0.007	0.581
<i>Salix alba</i>	3.859	10.458	0.620	1.888
<i>Xanthium strumarium</i> *	4.377	0.223	0.000	0.000
<i>Brachypodium sylvaticum</i>	0.764	3.330	0.000	2.057
<i>Paspalum distichum</i> *	3.741	0.075	0.000	0.000
<i>Lythrum salicaria</i>	0.808	0.161	0.080	0.009
<i>Leersia oryzoides</i>	3.094	0.044	0.000	0.000
<i>Acer negundo</i> *	0.368	3.889	0.000	2.779
<i>Urtica dioica</i>	3.345	11.904	0.087	8.430
<i>Echinochloa crus-galli</i>	4.282	0.241	0.609	0.038
<i>Arrhenatherum elatius</i>	0.063	7.502	2.278	4.048
<i>Phalaris arundinacea</i>	4.768	2.194	5.994	0.364
<i>Vulpia myuros</i>	0.248	0.676	0.121	2.677
<i>Rubus caesius</i>	0.711	1.072	0.442	4.758
<i>Artemisia vulgaris</i>	0.305	0.307	1.651	0.277
<i>Populus gr. nigra</i> (*)	7.957	3.028	4.879	15.251
<i>Agrostis stolonifera</i>	3.875	0.528	15.966	1.962
<i>Rorripa sylvestris</i>	1.729	0.000	2.893	0.245
<i>Galium aparine</i>	0.000	0.037	1.667	0.019
<i>Ludwigia grandiflora</i> *	0.167	0.000	1.487	0.009
<i>Erigeron annuus</i> *	0.040	0.190	1.138	2.939
<i>Poa pratensis</i>	0.000	0.000	0.000	4.464
<i>Elytrigia x intermedia</i>	0.000	0.000	0.007	5.654
<i>Tripleurospermum inodorum</i>	0.000	0.000	7.790	0.949
<i>Centaurea paniculata</i>	0.000	0.000	0.565	4.350
<i>Berteroa incana</i> *	0.000	0.000	3.804	1.578

**Figure 3.** Matrix of the mean observed relative cover (%) of each of the 29 most abundant species in the biogeomorphological and ecological successional phases of the fluvial biogeomorphological succession model, by river reach. The order of the species preserves the main floristic gradient (first axis of the correspondence analysis). Colours indicate a gradient of cover, from light blue (low) to dark red (high). Introduced (exotic) species are quoted with an asterisk.

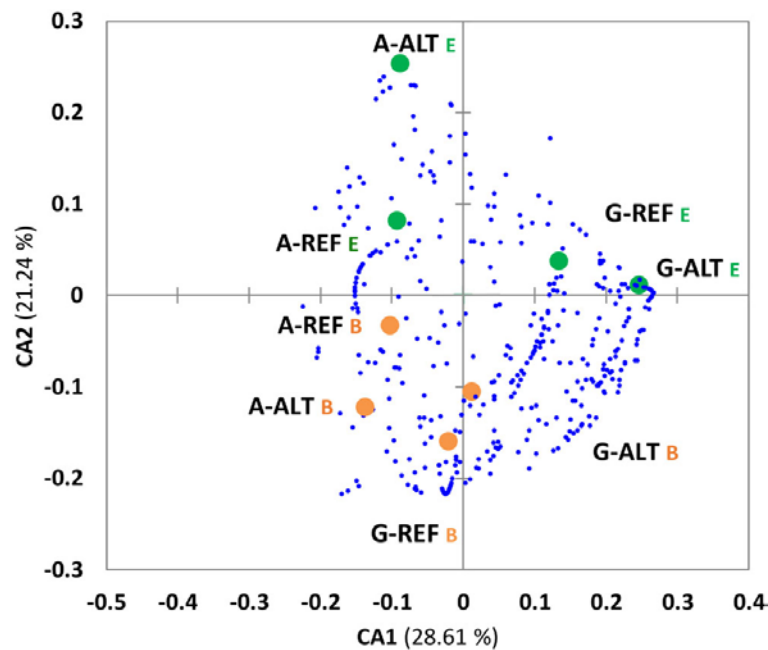


The B phases in each river reach tended to be more similar than the E ones (Figure 3, PERMANOVA,  $p < .001$ ). The floristic differences between rivers were significant (PERMANOVA,  $p < .001$ ; Table 2). Species scores across the bidimensional space (Figure 4) show that many species concentrated within the outer area of the cloud. This particular distribution indicates that a large number of species with low abundances participated in the ordination or, in other words, in the transition between successional phases and in the distinction between rivers. The first axis of the CA opposed xerophilous and thermophilous species (positive values, e.g., *Sedum album* and *Centaurea paniculata*) to those preferring fresher and wetter environments (e.g., *P. arundinacea* and *Agrostis stolonifera*). River identity was highly discriminated by CA1 but more for the E phase than for the B phase (CA1, Figure 4). CA2 was associated to the transition between the B and E phases, species, typical of the ecological phase such as *P. nigra* or *Fraxinus excelsior*, were positively loaded, whereas mostly pioneer species indicative of the biogeomorphological phase dominated the negative end (e.g., *Xanthium strumarium* and *Paspalum distichum*; CA2, Figure 4).

**Table 2.** Permutational multivariate analysis of variance table of results for species composition (Bray–Curtis similarity) indicating (columns) the source of variation in a type III model, the corresponding degrees of freedom ( $df$ ), the sum of squares (SS) and mean squares (MS), the pseudo- $F$ , and bootstrap/Monte Carlo permutation significance ( $p$  [perm]), numbers (unique perms), and associated probability values ( $p$  [MC]).

Source	$df$	SS	MS	Pseudo- $F$	$p$ (perm)	Unique perms	$p$ (MC)
Vegetation/habitat class	8	18,600	23,247	3.005	<b>.0001</b>	9,791	<b>.0001</b>
Study site type	1	19,589	9,794.7	2.736	<b>.0001</b>	9,812	<b>.0001</b>
River reach	1	25,055	25,055	2.715	<b>.0001</b>	6	<b>.0002</b>
Study site $\times$ Vegetation/habitat class	8	118,000	9,060.1	2.531	<b>.0001</b>	9,540	<b>.0001</b>
River reach $\times$ Vegetation/habitat class	8	93,880	13,411	1.753	<b>.0012</b>	9,811	<b>.0001</b>
Residuals	375	132,000	3,579.6	—	—	—	—
Total	401	1,860,000	—	—	—	—	—

Note. Effects are ranked according to pseudo- $F$  values (significant  $p$  values in bold).



**Figure 4.** Correspondence analysis of floristic data. Sample sites were identified with site codes (see main text) and with the considered fluvial biogeomorphological succession phases (B, biogeomorphological; E, ecological). Orange circles correspond to the centroid of sites for each river and type in the biogeomorphological phase and green ones to the ecological phase. Blue

dots correspond to species scores (plant species loadings). Percentage indicates the contribution of each axis to the total inertia.

When considering the most abundant species for all sites and river reaches (**Figure S1**), major floristic gradients separated distinctively the successional phases B and E. Contrast between B1 and B2 was due to the transition between drought-tolerant, ruderal species (*Rorripa sylvestris* and *T. inodorum*) and wetland species (*P. arundinacea* and *Echinochloa crus-galli*) and mesophilous prairies (*A. elatius* and *E. × intermedia*). However, hygrophilous grasses like *P. distichum* and *A. stolonifera* also dominated B1. The transition between B2 and B3 involved a reduced number of abundant species. However, the growth of young individuals of *P. nigra* and *S. alba*, together with a mixture of light-tolerant understory species (*U. dioica*, *Artemisia vulgaris*, and *X. strumarium*) and wetland grasses (*A. stolonifera*, *P. arundinacea*, and *E. crus-galli*) indicated a transition towards the B4 class. Distinctive species of the E1 class were subxerophilous species like *Anisandra tectorum*, *Vulpia myuros*, *B. incana*, *Erigeron annuus*, *S. album*, and *Sedum sexangulare*. On the river margins and floodplain, the transition between the E1 (for the Allier River only) and E2 classes was characterized by dominant mesophilous grasses (*Elymus repens*, *E. × intermedia*, *Poa pratensis*, *A. elatius*, and *Dactylis glomerata*) accompanied with mesophilous to subxerophilous ruderal forbs (*E. annuus*, *C. paniculata*, and *Saponaria officinalis*). The transition between E2 and E3 was marked by the presence or dominance of shrubs notably blackberries (*Rubus caesius* and *R. ulmifolius*). *P. nigra* showed similar abundance values in classes B4 and E4. Other tree species like *S. alba*, *Acer negundo*, *F. excelsior*, and *S. fragilis* showed higher abundances in E4 than in B4. Most of the abundant herbaceous species were shade-tolerant species like *U. dioica*, *Carex pendula*, and *Brachypodium sylvaticum*. They were more abundant in E4, whereas wetland or heliophilous species like *A. stolonifera*, *P. arundinacea*, and *X. strumarium* were more abundant in B4.

### 3.2 Species composition versus plant functional traits

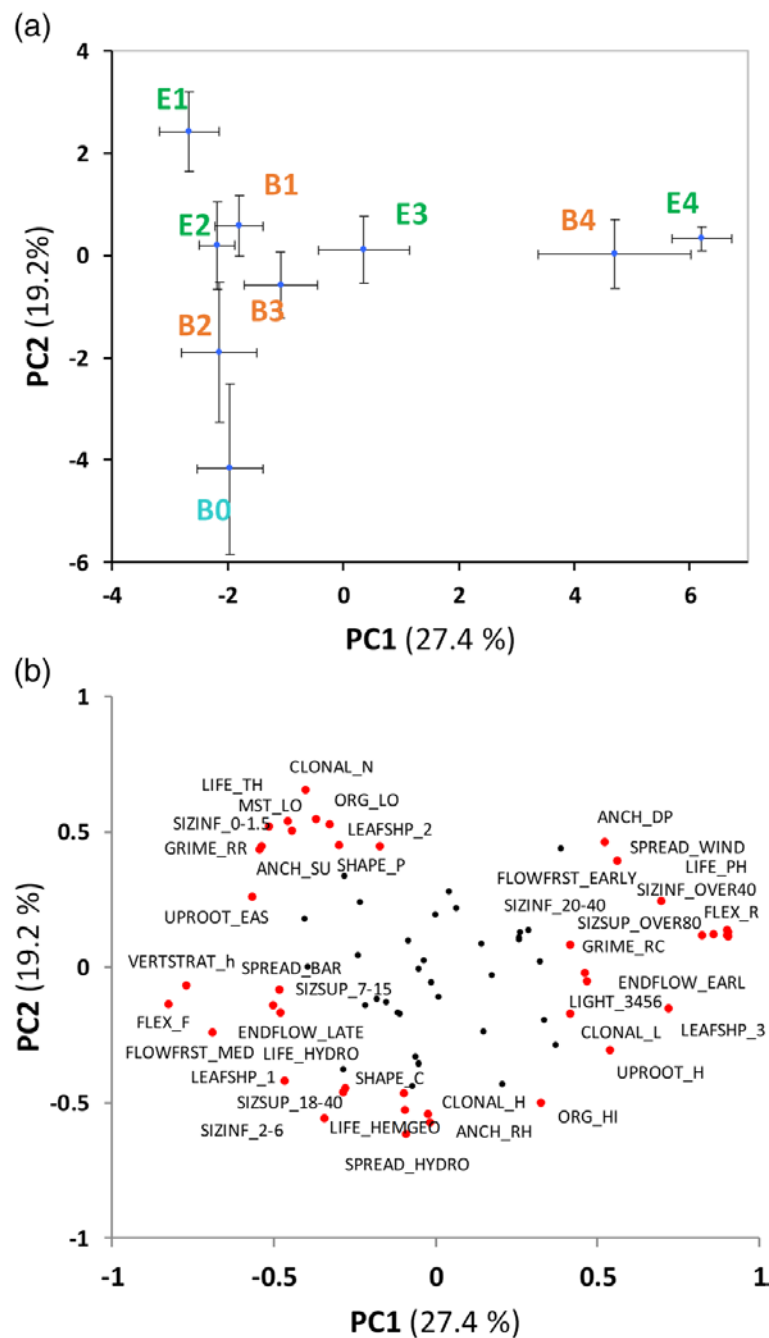
The analysis of floristic, as well as trait datasets, showed highly significant differences for all effects tested. For species composition, all the factors tested alone or in combination were significant (**Table 2**), although the “vegetation/habitat” effect contributed the most to the test (highest pseudo-*F* value). The PERMANOVA analysis calculated on traits (**Table 3**) showed that the effect of the FBS class became even more important (cf. pseudo-*F* values) than the other factors (source of variation) of the model. However, the effect of the reach (middle Garonne vs. lower Allier) remained significant but was not significant when combined with the effect of the vegetation/habitat class. The PERMANOVAs for plant traits calculated with community weighted mean (**Table 3**) and community weighted (not shown) gave identical results.

**Table 3.** Permutational multivariate analysis of variance table of results for trait composition calculated with community weighted mean (Bray–Curtis similarity) indicating (columns) the source of variation in a type III model, the corresponding degrees of freedom (*df*), the sum of squares (SS) and mean squares (MS), the pseudo-*F*, and bootstrap/Monte Carlo permutation significance (*p* [perm]), numbers (unique perms), and associated probability values (*p* [MC]).

Source	<i>df</i>	SS	MS	Pseudo- <i>F</i>	<i>p</i> (perm)	Unique perms	<i>p</i> (MC)
Vegetation/habitat class	8	159,000	19,921	8.056	<b>.0001</b>	9900	<b>.0001</b>
Study site type	1	9,846.8	4,923.4	3.530	<b>.0001</b>	9924	<b>.0003</b>
Study site × Vegetation/habitat class	8	36,609	2,816.1	2.019	<b>.0001</b>	9839	<b>.0001</b>
River reach	1	5,890E	5,892.2	1.280	.3229	6	.2903
River reach × Vegetation/habitat class	8	20,598	2,942.5	1.201	.2680	9913	.1990
Residuals	375	516,000	1,394.8	—	—	—	—
Total	401	839,000	—	—	—	—	—

Note. Effects are ranked according to pseudo-*F* values (significant *p* values in bold).

Multivariate analyses processed with taxonomic floristic (**Figure 4**) and trait (**Figure 5**) data ordinated the two FBS phases and the nine vegetation/habitat classes (from B0 to E4) in a similar way. Because the nine vegetation/habitat classes were aggregated for the floristic analysis (CA; **Figure 4**), CA shows a mean synthetic alignment of the two successional phases.



**Figure 5.** Principal component analysis calculated from community weighted means trait values of the reduced (20 traits and 78 modalities) dataset. (a) Mean ( $\pm$  95% confidence interval) of the site scores by vegetation/habitat class, illustrating the successional trajectories for the ecological (green) and biogeomorphological (orange) successional phases of the fluvial biogeomorphological succession model. (b) Species scores of the plant traits (more contributing traits ( $r > .5$ ) in red; others in black). Percentages indicate the proportion of the total variance explained by each axis. List of the relevant traits (see **Table S2** for complete trait list): ANCH\_DP, deep pivot root; ANCH\_RH, rhizomatous plant; ANCH\_SU, surficial rooting system; CLONAL\_H, highly clonal; CLONAL\_L, rarely clonal; CLONAL\_N, clonal type; ENDFLOW\_EARL, early blossoming end; ENDFLOW\_LATE, late blossoming end; FLEX\_F, high flexibility; FLEX\_R, high rigidity; FLOWFRST\_EARLY, early blossoming start; FLOWFRST\_MED, medium blossoming start; GRIME\_RC, ruderal and competitor; GRIME\_RR, strict ruderal; LEAFSHP\_1, very small or linear shaped leaves; LEAFSHP\_2, medium-sized leaves; LEAFSHP\_3, wide-shaped leaves; LIFE\_HEMGEO, hemigeocryptophyte; LIFE\_HYDRO, aquatic plant; LIFE\_PH, phanerophyte; LIFE\_TH,

therophyte; LIGHT\_3456, shade tolerant; MST\_LO, low soil moisture; ORG\_HI, high organic matter content; ORG\_LO, low organic matter content; SHAPE\_C, caespitose plant; SHAPE\_P, prostrate plant; SIZINF\_0–1.5, very small minimum size; SIZINF\_20–40, tall minimum size; SIZINF\_2–6, small minimum size; SIZINF\_OVER40, very tall minimum size; SIZSUP\_18–40, tall maximum size; SIZSUP\_7–15, medium maximum size; SIZSUP\_OVER80, very tall maximum size; SIZSUP-1\_3, small maximum size; SPREAD\_BAR, self-dispersed (barochore); SPREAD\_HYDRO, water-dispersed; SPREAD\_WIND, wind-dispersed; UPROOT\_EAS, very easily uprooted; UPROOT\_H, easily uprooted; VERTSTRAT\_h, herbaceous type; VERTSTRAT\_T, tree type.

The trait analysis (PCA; **Figure 5**) showed that early vegetation/habitat classes of the succession associated to the B phase and also to the E phase first appeared distinctively along axis PC1 (e.g., B0-2 and E1-2 had the most negative values on PC1) and the late vegetation/habitat classes (B4 and E4) had the most positive (PC1, **Figure 5a**). However, both B and E trajectories progressively converged along PC2 (i.e., early phases of both B and E) had the most loads in absolute terms (either positive or negative), but the late phases were the least contributing to the axis (E3, B4, and E4 had the lowest absolute values, PC2, **Figure 5a**). Thus, the two main gradients of the trait-based PCA showed a convergence in late vegetation/habitat classes of B (from B0 to B4) and E (from E1 to E4) trajectories (**Figure 5a**). The first gradient (PC1) corresponded to a successional gradient, whereas the second gradient (PC2) corresponded to a substrate moisture gradient opposing two outlier classes, that is, E1 (xerophilous and disconnected communities) and B0 (highly disturbed aquatic communities). The main relevant trait modalities for explaining PC1 were high flexibility, early flowering, easy uprooting, light and moisture affinity (negative values) versus large size, hard uprooting, late flowering, and low clonal capacity (positive values; **Figure 5b**). The most positively loaded traits along PC2 corresponded to an opportunistic ecological strategy, low clonal capacity, high organic matter content in soil, affinity to dry substrates, and narrow leaves.

## 4 Discussion

### 4.1 *A functional trait approach supports the comprehensive character of the FBS model because it can group successional classes and phases independently of regional differences*

Our results showed that within the same river reach as well as regionally (comparing two contrasted rivers), both species composition and plant traits can correctly discriminate a series of successional classes (a total of nine vegetation/habitat classes in this article) along the two larger successional phases (biogeomorphological [B] and ecological [E]) of the FBS model. However, trait characteristics were less affected by regional differences. First, the factor “river reach” was not significant in the PERMANOVA at the trait level, but it was significant at the taxonomic level. Second, we only detected differences in the plant community at the trait level between sites within a given river reach in one of the rivers analysed (the lower Allier River). These results highlight the convergence of similar strategies translated by similar plant traits of the different groups of species. Furthermore, it underpins that discrimination between the FBS phases should be based on a trait approach to better depict biogeomorphological groups of response to and effect on hydrogeomorphological processes and landforms (Corenblit et al., 2015; Diehl et al., 2017; O’Hare et al., 2016). We see this result as a further contribution to our understanding that the FBS model is widely relevant for rivers in the temperate zone and perhaps beyond.

### 4.2 *Limitations of the functional trait approach to inform the FBS model*

The trait-based approach could not discriminate well between reference and altered sites. We propose three explanations. First, the contrast between reference and altered sites from the same river was too weak to be highlighted. This was clearly the case along the middle Garonne River, overall more channelized than the lower Allier River. Second, the large number of opportunistic species associated to landscape connectivity implies functional redundancy within different communities. This hypothesis was identified by Fraaije, ter Braak, Verduyn, Verhoeven, and Soons (2015) as an overlooked process for explaining vegetation gradients in the riparian context. Third, both human and natural disturbances filtered species from the same functional pool, increasing the chances of reference and altered sites to present similar species characteristics of the same functional pool and hence with

similar plant traits. This hypothesis is supported, at least for pioneer stages typical of the biogeomorphological phase, by the positive correlation observed between disturbance-dependent native and exotic ruderal species (Corenblit et al., 2014; Tabacchi & Planty-Tabacchi, 2005).

Despite the weak discrimination between reference and altered sites using the trait approach, this approach was successful in discriminating between the two successional phases of the FBS model and the associated vegetation/habitat classes. Nevertheless, we suggest that there is still room for improvement. First, certain traits that could not be included in this study were considered as fundamental by other authors, as, for example, the SLA (specific leaf area) and seed mass (Westoby, 1998) or the biovolume and the canopy frontal area (Corenblit et al., 2009; Diehl et al., 2017; O'Hare et al., 2016). In particular, biomechanical traits could have emphasized plant effects within the feedback loops between hydrogeomorphological processes and vegetation succession and could have helped to obtain an even better discrimination of the two successional phases. Identifying key response and effect traits involved in biogeomorphological feedbacks with experiments must become a priority (Garófano-Gómez et al., 2016). Second, we followed the approach of many studies that have used traits as theoretical and unique values for the species themselves, taken from the literature, and not from direct field measurements (Violle et al., 2007). The use of in situ measured traits might have revealed a higher in-between site variability and therefore improved the discrimination of successional phases and may be helping to discriminate the reference and altered sites. Species phenotypic plasticity may potentially induce a strong variability in plant response and effect traits. Here, the coupling between the taxonomic (stable reference) and the trait approach (plastic reference) must be relevant for studying such a variability. To a certain extent, our analysis probably has also been biased by assigning adult traits to populations with variable growth stages. This can be problematic for woody pioneer Salicaceae species, which are the main ecosystem engineers along the Garonne (Corenblit et al., 2016) and the Allier (Hortobágyi, Corenblit, Steiger, & Peiry, 2018) rivers, and show a high variability of traits and physiognomy between their growth forms (Corenblit et al., 2014; Kerkhoff, Fagan, Elser, & Enquist, 2006). Furthermore, we aggregated individual traits at the community scale, as recommended by Ackerly and Cornwell (2007). However, we recognize that such aggregations might not be recommendable in all cases because traits do not necessarily have additive effects at the local scale according to spatial arrangements.

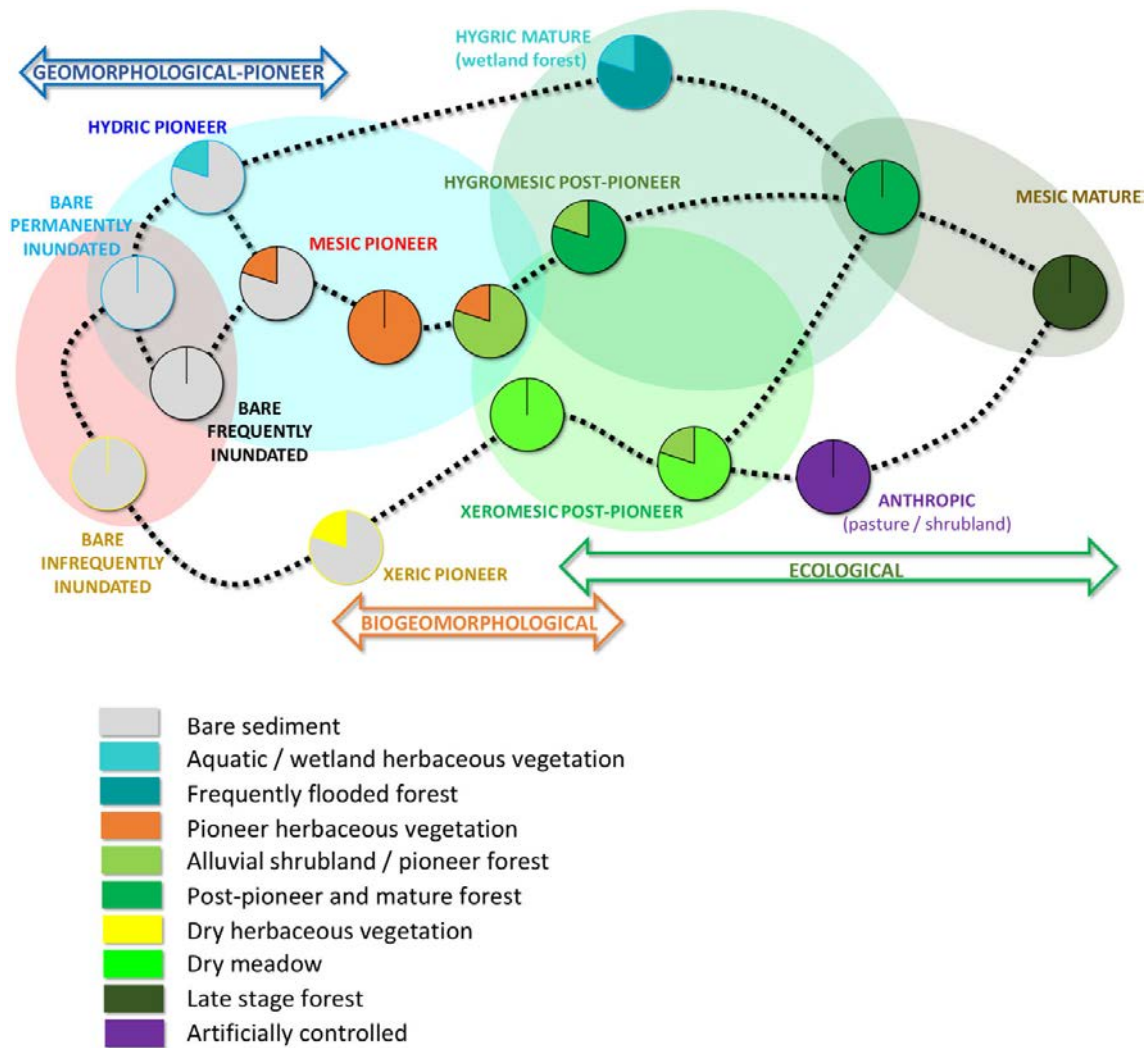
#### 4.3 *A conceptual model for multiple successional trajectories in river corridors of the temperate zone*

Our results contributed to a better understanding of the multiple successional trajectories that can occur in river corridors of the temperate zone. Some communities typical of early successional stages, such as pioneer communities dominated by *P. nigra*, can reveal a strong resistance to flood events (Corenblit et al., 2016). Such resistance can drive the system towards biogeomorphological metastable states with tipping points of reversibility linked to the relation between the flood regime and biomechanical plant traits. Such metastability implies that the succession can suddenly be reinitialized or rapidly progress within the entire river corridor (Corenblit, Steiger, & Tabacchi, 2010). The examples of the Allier and Garonne rivers suggest that sharp transitions between the B and E phases can occur when lateral channel dynamics are strong, for example, during meander translations, as well as when the river is incising, both resulting in a hydrological disconnection of large areas or small patches within the river corridor. Therefore, such decoupling can also directly affect the FBS trajectories.

In the present study, all successional trajectories initiated at hygric, subxeric, or mesic pioneer stages converged to very similar mature stages, from both a taxonomic (floristic) and a functional (trait) point of view (**Figure 6**). This could be explained by the high ecological plasticity of some species involved in these mature stages, especially *P. nigra*, which plays also a pivotal role in the pioneer and postpioneer B stages (Dufour, 2005; Corenblit et al., 2014, 2016). Patterns not specific to the described FBS model, manifested by the existence of the E1 class only on the Allier River, where the deposits of coarse, permeable sediment facilitated the colonization by subxerophilous species (Garófano-Gómez et al., 2017), reflected the role of hydrogeomorphological processes in creating the suitable habitat.

The successional patterns observed along the Allier and Garonne rivers probably comprise a combination between successional trajectories with multiple possible pathways within and between the B and E phases that may be applicable elsewhere (**Figure 6**). Differences between the B and E phases could be subtler or more pronounced than in our study, depending on the connectivity between channel and floodplain habitats and

hydrogeomorphological disturbances. Some successional trajectories like the ones related to the B0 class (cut-off channels and standing waterbodies) initially strongly exposed to disturbance but keeping a high moisture degree or starting from the E1 class (channel margins and upper banks), sharply disconnected by strong sediment deposition, could be classified as extreme situations in this general scheme. Other converging pathways were identified earlier, within the FBS model (Corenblit et al., 2009), as well as by other authors, without referring to the FBS model (Bendix & Hupp, 2000; Egger et al., 2015). This stresses the importance of identifying specific physical (hydrogeomorphological) and/or biological drivers for the successional pathway or trajectory considered (Muñoz-Mas et al., 2017).



**Figure 6.** Conceptual scheme of plant succession in the middle Garonne and lower Allier rivers. Each characteristic plant successional unit is represented by a circle, from pioneer (left) to mature (right) stages, with the proportion of bare sediment in grey. The three horizontal arrows indicate the main phases of the fluvial biogeomorphological succession model. The location of each unit on the Y axis corresponds to a dry (bottom) to wet (top) gradient. The ellipses are putative groupings from highly reversible states to more stable states. The dotted lines indicate preferential trajectories.

## 5 Conclusion

This study shows the complementarity of the species composition and the plant trait-based approaches in discriminating the biogeomorphological and ecological phases of the FBS model. The trait approach has proven useful in distinguishing between the two successional phases of the FBS model and the associated vegetation/habitat classes but much less so in discriminating between reference and altered sites, suggesting a lower than expected functional contrast between the four sites. We point out the necessity to detect subtle

differences in gradients or bifurcations within successional trajectories resulting from local particularities (from river reach to microhabitat), for example, in order to quantify vegetation resilience facing short- and long-term environmental change. In conclusion, our results contribute to a better understanding of the multiple successional trajectories that can occur in midlatitude river corridors. The specific conditions and time spans necessary for the vegetation to progress and regress between pioneer and mature stages were need to be known in order to universally apply the functional trait approach to discriminate the phases of the FBS model. Relating plant traits to their effects on fluvial landform dynamics remains a core challenge in explaining succession including feedback mechanisms between hydrology, morphodynamics, and vegetation dynamics.

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## Conflict of interests

The authors declare no conflict of interests.

## Data availability statement

The data underpinning this research are available from the lead author upon request.

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## Supporting information

**Table S1.** Number of plots for all nine vegetation/habitat classes (columns) and river systems compared (lines).

River system	B0	B1	B2	B3	B4	E1	E2	E3	E4	Total
Allier River	8	42	20	11	6	26	39	5	25	182
Garonne River	10	56	4	43	33	0	15	34	25	220
Total	18	98	24	54	39	26	54	39	50	402

**Table S2.** Biological and ecological traits used in this study before (initial) and after (final) post-hoc trait selection from correlation and multicollinearity analyses.

Acronym	Definition	Initial no. of modalities	Final no. of modalities	Reference
SHAPE	Above-ground individual architecture	9	6	Tison and de Foucault (2014)
FLEX	Above-ground organs flexibility, woodiness	6	3	Derived from Tison and de Foucault (2014)
ANCH	Below-ground architecture	8	6	Tison and de Foucault (2014)
UPROOT	Susceptibility to uprooting (assuming medium drag force on medium-grained substrate)	5	3	Derived from Tison and de Foucault (2014)
POLLIN	Pollination mode	11	0	Julve (2016)
SPREAD	Dispersal mode	8	4	Julve (2016)
LIFE	Life forms/biological types	22	9	Tison and de Foucault (2014)
LEAFSHP	Individual leaf size and shape	22	3	Tison and de Foucault (2014)
GRIME	Level two Grime's strategy	9	5	Grime (2001)
AIRMST	Air moisture preference	10	0	Ellenberg et al. (1992)
MST	Substrate moisture preference	12	3	Ellenberg et al. (1992)
CONT	Continental preference	8	0	Ellenberg et al. (1992)
ORG	Substrate organic matter content preference	9	3	Ellenberg et al. (1992)
SOILTEXT	Substrate grain size preference	9	2	Ellenberg et al. (1992)
LIGHT	Light exposure preference	9	2	Ellenberg et al. (1992)
TEMP	Temperature preference	9	0	Ellenberg et al. (1992)
PH	Substrate acidity preference	9	0	Ellenberg et al. (1992)
SALT	Tolerance to edaphic salinity	8	0	Ellenberg et al. (1992)
TROPH	Substrate nutrient content preference	9	2	Ellenberg et al. (1992)
SIZINF	Minimum adult size	24	5	Tison and de Foucault (2014)
SIZUP	Maximum adult size	33	6	Tison and de Foucault (2014)
FLOWFRST	Earlier blooming period	10	4	Tison and de Foucault (2014)
ENDFLOW	Late blooming period	11	3	Tison and de Foucault (2014)
CLONAL	Type of vegetative multiplication	3	3	Tison and de Foucault (2014)
VERTSTRAT	Vertical layer at the adult stage	6	5	Tison and de Foucault (2014)

ORIGIN	Biogeographic origin (native or introduced)	2	1	Tison and de Foucault (2014)
Total number of traits		26	20	
Total number of trait modalities		283	78	

Species	B1	B2	B3	B4	B0	E1	E2	E3	E4
<i>Hedera helix</i>	0.00	0.00	0.00	0.72	0.00	0.00	0.00	0.00	1.94
<i>Lamium maculatum</i>	0.00	0.00	0.04	1.28	0.00	0.00	0.00	0.00	2.64
<i>Impatiens glandulifera</i> *	0.00	0.00	0.00	1.31	0.00	0.00	0.00	0.13	2.34
<i>Brachypodium sylvaticum</i>	0.00	0.00	0.13	3.33	0.00	0.00	0.00	0.31	9.46
<i>Acer negundo</i> *	0.02	0.00	0.04	1.59	0.00	0.00	0.00	0.00	13.40
<i>Stachys sylvatica</i>	0.00	0.00	0.02	0.31	0.00	0.00	0.00	0.03	3.78
<i>Carex pendula</i>	0.00	0.04	0.04	0.69	0.00	0.00	0.00	0.13	1.70
<i>Glechoma hederacea</i>	0.00	0.00	0.02	3.56	0.00	0.00	0.02	0.49	3.14
<i>Galium aparine</i>	0.03	0.04	0.04	0.95	0.00	0.00	0.00	0.41	2.90
<i>Fraxinus excelsior</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.82
<i>Acer pseudoplatanus</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.20
<i>Salix alba</i>	0.18	0.67	3.35	12.69	0.89	0.00	0.00	0.00	18.00
<i>Urtica dioica</i>	0.02	0.08	2.15	10.69	0.17	0.00	0.19	7.87	26.12
<i>Populus nigra</i>	0.37	0.50	4.67	40.59	0.89	0.04	0.30	1.95	32.90
<i>Alanthus altissima</i> *	0.00	0.00	0.02	7.36	0.00	0.00	0.00	0.00	0.20
<i>Ulmus minor</i>	0.00	0.00	0.00	0.44	0.00	0.00	0.30	0.77	1.52
<i>Alnus glutinosa</i>	0.00	0.00	0.00	0.00	0.83	0.00	0.00	0.00	1.70
<i>Rubus caesius</i>	0.02	0.00	0.50	3.18	1.11	1.27	1.22	3.46	5.80
<i>Rubus ulmifolius</i>	0.00	0.00	0.00	0.13	0.00	0.00	0.00	10.03	0.86
<i>Phalaris arundinacea</i>	0.85	10.88	5.63	8.00	3.78	0.00	0.00	3.13	2.26
<i>Xanthium strumarium</i> *	0.06	0.46	6.37	6.23	1.50	0.00	0.02	0.46	0.00
<i>Lythrum salicaria</i>	0.11	0.42	1.91	0.36	0.17	0.00	0.02	0.00	0.28
<i>Bidens frondosa</i> *	0.26	0.25	0.76	0.74	1.17	0.08	0.00	0.08	0.14
<i>Reynoutria x Bohemica</i> *	0.00	0.00	0.04	0.15	0.00	0.19	0.56	1.67	0.40
<i>Artemisia verlotiorum</i> *	0.00	0.00	3.13	0.62	0.00	0.00	0.00	5.26	0.00
<i>Buddleja davidii</i> *	0.00	0.00	0.00	0.13	0.00	0.00	0.00	3.33	0.00
<i>Galium palustre</i>	0.00	0.00	0.00	0.00	3.33	0.00	0.00	0.00	0.12
<i>Persicaria lapathifolia</i>	0.16	1.42	2.83	0.62	1.78	0.19	0.19	0.08	0.82
<i>Echinochloa crus-galli</i>	0.29	2.96	6.02	3.59	1.44	0.15	0.00	0.64	0.02
<i>Cyperus eragrostis</i> *	0.26	0.25	2.13	0.18	0.06	0.00	0.00	0.00	0.00
<i>Salix purpurea</i>	0.18	2.21	0.13	0.64	0.06	0.04	0.46	2.95	0.14
<i>Agrostis stolonifera</i>	3.13	17.75	5.26	1.54	9.28	0.54	0.74	0.64	3.08
<i>Leersia oryzoides</i>	0.11	2.29	2.91	0.21	2.28	0.00	0.00	0.00	0.06
<i>Potamogeton nodosus</i>	0.02	0.00	0.00	0.00	6.39	0.00	0.00	0.00	0.00
<i>Ceratophyllum demersum</i>	0.08	0.00	0.00	0.00	3.50	0.00	0.00	0.00	0.00
<i>Dactylis glomerata</i>	0.00	0.29	0.06	0.03	0.00	0.00	1.52	0.44	0.22
<i>Paspalum distichum</i> *	0.87	2.71	6.30	0.41	7.39	0.00	0.04	0.03	0.00
<i>Ludwigia grandiflora</i> *	0.08	4.00	0.00	0.13	5.89	0.00	0.02	0.00	0.00
<i>Saponaria officinalis</i>	0.16	0.25	3.04	0.54	0.28	0.04	1.89	1.92	0.00
<i>Elytrigia repens</i>	0.00	0.00	0.69	0.08	0.00	0.00	8.02	0.72	0.22
<i>Elodea canadensis</i> *	0.00	4.58	0.00	0.00	0.56	0.00	0.00	0.00	0.02
<i>Artemisia vulgaris</i>	0.81	0.50	1.15	0.44	0.00	1.04	0.04	0.56	0.00
<i>Rosa gr. Canina</i>	0.00	0.00	0.00	0.44	0.06	0.96	0.57	0.56	0.00
<i>Rorripa sylvestris</i>	1.81	2.38	1.78	0.92	1.67	0.62	0.19	0.00	0.00
<i>Anisantha tectorum</i>	0.00	0.00	0.00	0.26	0.00	3.42	0.17	0.00	0.00
<i>Rumex thyrsoiflorus</i>	0.03	2.33	0.69	0.38	0.28	1.35	1.81	0.15	0.12
<i>Hypericum perforatum</i>	0.50	0.13	0.06	0.26	0.00	0.65	1.31	0.97	0.00
<i>Tripleurospermum inodorum</i>	1.45	5.67	2.50	0.00	0.00	0.04	1.02	0.64	0.00
<i>Elytrigia x intermedia</i>	0.00	0.00	0.02	0.00	0.00	0.00	8.83	0.00	0.00
<i>Bertoreia incana</i> *	0.85	0.71	2.65	0.13	0.06	2.73	1.46	0.13	0.00
<i>Pilosella peliseriana</i>	0.50	0.00	0.02	0.00	0.00	2.77	0.20	0.00	0.00
<i>Vulpia myuros</i>	0.10	0.17	0.46	0.15	0.00	6.42	1.91	0.82	0.00
<i>Microporum tenellum</i>	0.08	0.00	0.02	0.00	0.00	3.85	0.28	0.00	0.00
<i>Poa pratensis</i>	0.00	0.00	0.00	0.00	0.00	1.23	5.98	0.51	0.00
<i>Erigeron annuus</i> *	0.34	1.83	0.44	0.10	0.06	8.08	0.87	0.28	0.00
<i>Arrhenatherum elatius</i>	0.00	3.38	0.15	0.00	0.00	1.73	14.80	0.59	0.02
<i>Trifolium arvense</i>	0.00	0.00	0.00	0.00	0.00	1.15	1.41	0.03	0.00
<i>Elytrigia campestris</i>	0.00	3.17	0.00	0.05	0.00	1.69	3.09	0.00	0.00
<i>Centaurea paniculata</i> *	0.90	0.42	0.20	0.00	0.06	2.08	6.76	0.77	0.00
<i>Sedum album</i>	0.00	0.29	0.46	0.00	0.28	3.92	1.52	0.00	0.00
<i>Sedum sexangulare</i>	0.00	0.83	0.00	0.00	0.28	4.88	1.98	0.00	0.00

**Figure S1.** Mean observed relative cover (%) of the 60 most abundant species in each of the vegetation/habitat classes (columns), all sites included. The column order corresponds to a successional sequence from pioneer to mature stages, class B0 (wetland vegetation) corresponding to an outlier in this sequence. Colours indicate the degree of relative cover by each species (in total 5 classes, from low cover in light blue to high cover in dark red).

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