



## RESEARCH ARTICLE

# Road-River Intersections (Bridges) Negatively Affect Plant Species Diversity and Ecological Attributes

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## ABSTRACT

**Question:** Linear habitats are terrestrial and aquatic corridors that can be natural or anthropogenic. Here we asked: how does the intersection of two types of linear habitats (roads and rivers) affect plant species diversity, composition and ecological attributes?

**Location:** Southern France.

**Methods:** We studied road-river intersections (bridges) to test how composition, alpha and beta diversity, and ecological preferences of species in both roadside and riverside plant communities responded to the influence of bridges. We also used spatial predictors (spatial eigenvector maps) to assess whether bridges influenced directional spatial processes (upstream-downstream river axis) structuring community composition.

**Results:** We showed that vegetation around bridges differed from that away from bridges in terms of species composition and ecological preferences, and reduced alpha and beta diversities. We also found a convergence of species' ecological preferences in plant communities of rivers and roads at bridges. The turnover component of species beta diversity was lower at bridges, presumably due to different disturbance regimes, leading to biotic homogenization. However, our results show that the impact of bridges on directional spatial processes affecting species composition was negligible.

**Conclusion:** The strong effect of bridges as selecting forces of plant communities for both rivers and roads suggests bridges should not be overlooked. Our findings will help the development of more effective management of both types of linear habitats for the conservation of the plant species they host and the associated ecological functions and ecosystem services they provide.

## 1 | Introduction

Linear habitats consist of terrestrial and aquatic corridors, which can be natural such as hedgerows, grass strips and rivers or anthropogenic, like roads, railway lines and canals. These habitats are commonly considered in biodiversity and environmental management policies. For example, the European Blue-Green Infrastructure policy (BGI, “green” vegetation, and “blue” water spaces) prioritizes strategically planned networks where different linear habitats intersect to enhance connectivity and possibly biodiversity and ecosystem services (European Union Commission 2013). At the landscape scale, maintaining well-connected habitats to function as ecological corridors might be beneficial for biodiversity in the context of climate change, by facilitating species dispersal toward new suitable refuge areas, or acting as refugia themselves (Smart, Marrs, et al. 2006; Smart, Thompson, et al. 2006; Villemey et al. 2018). However, at local scales, a high degree of connectivity can be detrimental, due to the increased spread of invasive species (Glen, Pech, and Byrom 2013), and, from a metacommunity perspective, beta diversity can also be negatively affected because high levels of dispersal can contribute to biotic homogenization (Mouquet and Loreau 2002). Although the importance of managing linear features at the landscape scale to optimize biodiversity is well recognized (Tiang et al. 2021; Dilts et al. 2022), the role of intersections in enhancing or reducing connectivity among different linear corridors remains largely unexplored.

Rivers and roads are linear habitats of great ecological and social importance. Rivers supply multiple ecological functions and ecosystem services, such as nutrient, sediment, and water flow control, support for biodiversity and climate regulation (Tabacchi et al. 1998; Hood and Naiman 2000; Décamps 2011). In parallel, most of the planet is fragmented by roads (Ibisch et al. 2016), and their extension is projected to increase by more than 60% from 2010 to 2050 (Dulac 2013). In contrast to river corridors, road corridors cause landscape fragmentation (Niu et al. 2018), with potentially negative consequences for biodiversity (Laurance and Vasconcelos 2009; Gardiner et al. 2018), carbon storage and water regulation (Molina et al. 2023). Yet, roads are also potential corridors for wildlife, in some cases hosting rare and threatened species (Gardiner et al. 2018; Wagner, Metzler, and Frye 2019).

Rivers and roads intersect at bridges. Bridges can create specific environmental constraints that impact plant communities and species dispersal. Some constraints, such as the clearing of vegetation for safety and maintenance, which reduces local biomass affect both roads and rivers. In rivers, in addition to the presence of bridge piers, the installation of rip-raps, which are protective barriers of rocks and concrete used to stabilize the river bank and secure the bridge foundation, may increase hydraulic turbulence and the effects of flooding (Richardson et al. 2007; Vallet et al. 2010; Kowarik 2011; Reid and Church 2015). The steel-concrete composite pavement characteristic of bridges increases substrate and air temperature more than usually found along roads (Godefroid and Koedam 2007). These effects caused by bridges and their related environmental constraints can also promote further biotic homogenization of plant communities by filtering species

with specific ecological preferences and reducing overall functional diversity (Cornwell, Schwillk, and Ackerly 2006; Costa et al. 2017). Because bridge effects could impact both roads and rivers, ecological traits of plant communities of these two types of habitats are expected to converge at bridges (Perry, Reynolds, and Shafroth 2018; Travers, Härdtle, and Matthies 2021).

The local community composition of rivers and roads are affected by a unique set of environmental constraints. Riverside ecosystems (or riparian zones) are strongly affected by hydrological disturbances related to water level fluctuations and fluvial erosion-deposition processes, affecting species composition and leading to hyper-diverse plant communities (Naiman and Décamps 1997; Bornette et al. 2008; González et al. 2019). The dynamic nature of riparian zones facilitates species colonization, including non-native and invasive species from the surrounding areas (Décamps, Planty-Tabacchi, and Tabacchi 1995; Hood and Naiman 2000; Tabacchi and Planty Tabacchi 2001; Richardson et al. 2007). The species composition of riparian zones is also affected by environmental conditions, which filter species associated with particular ecological preferences such as wet soils and high nutrient availability (Janssen et al. 2021). Similarly, roadsides are prone to frequent physical disturbances, high nutrient input, traffic flow and volume and human-mediated dispersal of propagules (Von Der Lippe and Kowarik 2008; Fernández-Murillo, Rico, and Kindlmann 2015; Lemke, Kowarik, and von der Lippe 2018). In addition to high disturbance, high nutrient availability, low soil moisture and high temperature typical of roadside habitats may act as environmental filters, favoring some species, and disfavoring others (Truscott et al. 2005; Lee, Davies, and Power 2012; Čepelová and Münzbergová 2012). However, it is still unknown how the ecological preferences of species on roads and rivers can be affected by additional environmental constraints caused by the presence of bridges.

Plant community composition can be spatially structured by directional and non-directional spatial patterns. A directional upstream-to-downstream gradient is typically the main factor structuring riparian plant communities because of its overarching influence on water, sediments, nutrient fluxes, and dispersal of propagules (Nilsson et al. 2010; Bourgeois et al. 2016). However, directional processes may not be as important in structuring plant communities along regulated and fragmented rivers, as the capacity of linear habitats to act as corridors of propagules depends on the distance an organism can travel between connected sites, but also on modifications to the river system (e.g., dams, culverts, channelization, and bridges) (Ward 1995; Nilsson and Svedmark 2002; Aronson et al. 2016). Road corridors also disperse plants through vehicle movements (Von Der Lippe and Kowarik 2008; Lemke, Kowarik, and von der Lippe 2018) and road maintenance activities (Christen and Matlack 2009), but these are not unidirectionally oriented when considering two-way roads. Dominant patterns of spatial variability can be studied with eigenvector maps (Blanchet, Legendre, and Borcard 2008; Blanchet et al. 2011), when either a directional forcing process is expected (Asymmetric Eigenvector Maps, AEM) or no main directionality is hypothesized (Moran's Eigenvector Maps, MEM). However, to our knowledge, AEM has been

used to investigate plant community composition along river systems (e.g., Bourgeois et al. 2016; Brice, Pellerin, and Poulin 2016; Henry et al. 2018), but never along other terrestrial linear habitats or to understand the effect of road-river metacommunities.

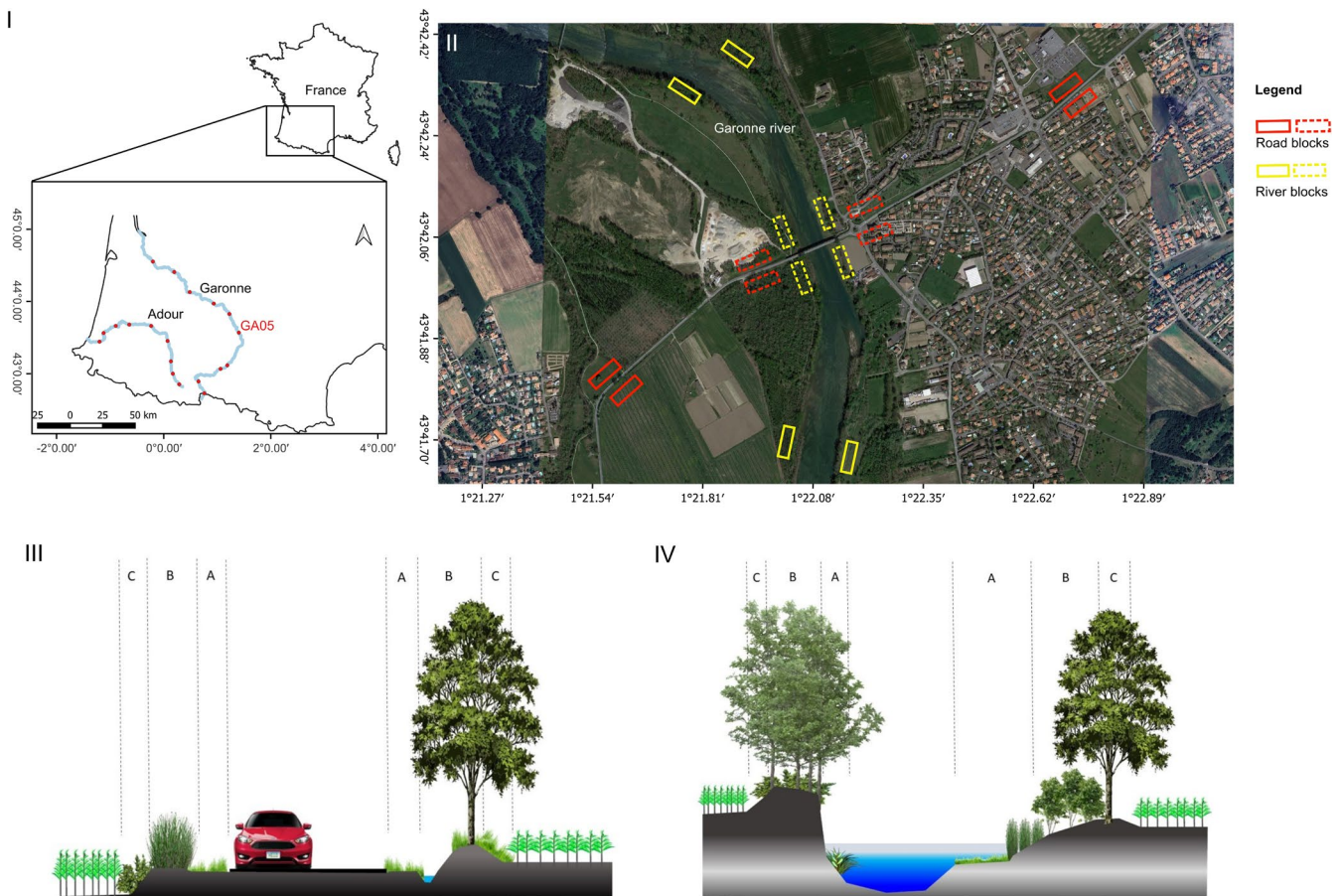
With the construction of an increasing number of roads to fulfill rising transportation needs and considering the increasing vulnerability of riparian communities, it is, therefore, important to better unravel the effect of bridges on road and river plant communities. This understanding will inform more effective management of both types of linear habitats for the conservation of the plant species they host and the associated ecological functions and ecosystem services they provide. It can also help to develop more integrative, conjoining management policies, considering distinct corridor types and their interactions. Focusing on two river systems in southern France, we tested the response of diversity and ecological preferences to the bridge influence on the roadside and riverside vegetation, while controlling for climate, soil, environmental and land cover variables. More specifically, we asked as following: (1) Are the alpha and beta diversities of plant communities affected by bridges? (2) Do environmental filters at bridges favor species with similar ecological preferences, leading to trait convergence, compared to plant

communities on river and roadsides away from bridges? And finally: (3) Are directional spatial processes more important than non-directional spatial processes in structuring riverside and roadside species composition, and do bridges influence the effect of directional spatial predictors on species composition?

## 2 | Material and Methods

### 2.1 | Study Area and Vegetation Surveys

The study area was the Adour-Garonne administrative basin (approx. 116,000 km<sup>2</sup>), which occupies most of the southwest of France (Figure 1). Both the Adour (approx. 330 km long, elevation gradient: 2876 m) and the Garonne (approx. 650 km, elevation gradient: 2360 m) rivers have their sources in the Pyrenees Mountain range (on the Spanish side for the Garonne), and flow in a NW direction through a very diverse territory including a wide elevational range toward their confluence with the Atlantic Ocean at the cities of Bayonne (Adour) and Bordeaux (Garonne), respectively. The road network in France contains over 1 million km and is the longest and one of the densest in the European Union (Ouedraogo et al. 2020). The sample design was built considering the



**FIGURE 1** | Overview of the study sites illustrating: (I) sample area in the southwest of France and the location of the 19 sample sites along the Adour and the Garonne rivers, (II) location of the river and road blocks by the bridge (dotted lines) and far from the bridge (reference, solid lines) displaying the GA05 site as example (location of reference and bridge blocks are illustrative to facilitate visualization), (III) illustration of the zones' disposition on the road, and (IV) on the river. The three zones (A, B, C) are distinguished within each block. The five quadrats forming a transect within each zone are not represented in the figure. Google Image 2023.



following hierarchy, detailed below: site>block>zones>quadrats. We selected nine sites along the Adour River (AD01–AD09) and 10 sites along the Garonne River (GA01–GA10) with approximately 30 km distance separating two consecutive sites along each river (Figure 1I). Each site was centered on a bridge, but we distinguished “bridge” sampling locations on each corridor (road or river, 20 m apart from the bridge), and a “reference” location, representative of the control locations along each corridor (1 to 2 km from the bridge structure). This set-up resulted in 16 sampling blocks per site: 8 on the roadside, and 8 on the riverside. Blocks were distributed on both sides upstream and downstream from the bridge along the river, and on both sides before and after the bridge along the road (see Figure 1II), totalling 304 blocks (19 sites  $\times$  16 blocks).

Three zones (or strips) were distinguished within each block: an internal (A), an intermediate (B) and an external zone (C; Figure 1III,IV). The internal zone (A) of roads corresponded to the vegetated part in contact with the asphalt roadway (i.e., berm). It is the most frequently mown, and therefore hosts only herbaceous species. For rivers, it corresponded to the most frequently flooded habitats, directly in contact with the main water channel. Zone A of rivers can be colonized by herbaceous or shrubby vegetation, but also occupied by pioneer or late-successional tree vegetation. The intermediate zone (B) of roads may or may not include a drainage ditch. For the river, zone B was associated with a variety of habitats. The external zone (C) represented the edge between the linear habitats (road or river) and the surrounding landscape. For roads, it could host planted trees. For rivers, this edge marked the boundary with a riparian-terrestrial habitat.

At each zone of each block, we set up study transects that consisted of five quadrats of  $2 \times 0.5$  m ( $1 \text{ m}^2$ ) separated by 1.5 m. Transects within each zone run parallel to the corridor. In total, 4560 quadrats were surveyed in the summer of 2015. For each of these quadrats, sampling consisted of the identification and the visual estimation of the relative cover of all plant species. Bare substrate cover was also recorded. Taxonomic nomenclature followed Flora Gallica (Tison and de Foucault 2014).

## 2.2 | Plant Community (Response) Variables

For each quadrat, we calculated species richness and Shannon diversity of the plant community to quantify alpha-diversity patterns. We also calculated beta diversity across all quadrats per block ( $\beta$ Block), and across all quadrats per zone within each block ( $\beta$ ZoneA,  $\beta$ ZoneB, and  $\beta$ ZoneC). For these metrics, we used the quantitative forms of Jaccard-based indices (Legendre 2014) using the equations of Baselga (2013), as implemented in the function “beta.div.comp()” in the “adespatial” R package (Dray et al. 2021). We also partitioned all  $\beta$ -diversity measures to separate the contribution of species turnover or replacement ( $\beta$ Turn) from the nestedness component ( $\beta$ Ne), which reflects composition dissimilarities due to species richness differences (Baselga 2013; Legendre 2014).

In addition to these measures of taxonomic diversity, we also retrieved information on species (1) traits, (2) ecological

preferences and (3) disturbance responses from several public databases. First, as species traits, we identified the life span of all species (short vs. long-lived), and retrieved data on species dispersal modalities from the Baseflor database (Julve 2015). We also included species native (native vs. non-native) and invasive (invasive vs. non-invasive) status according to the French National Botanical Conservatory (CBN) and regional lists (Caillon and Lavoué 2016; Cottaz and Dao 2021). Second, to describe species ecological preferences, we extracted Ellenberg's indicator values (EiV, Ellenberg et al. 1991) from the Baseflor database (Julve 2015). Ellenberg's indicator values are based on a simple ordinal classification of plants according to the position of their realized ecological niche along an environmental gradient. They give information about the performance of a plant in its realized niche and represent estimates of species ecological optima along the main ecological gradients. Specifically, we considered the following seven EiV related to environmental, climatic and substrate preferences: light, nutrient and soil moisture (resource availability), air moisture and temperature (climate), organic matter content and soil texture (soil properties). Third, we used indicator values of species' optimal positioning along disturbance gradients (see Midolo et al. 2023) based on their responses to mowing and soil physical disturbances (DiV).

We then quantified functional diversity using the EiV and DiV of species within each quadrat. To assess functional diversity and identify if species within quadrats responded similarly to environmental constraints (trait convergence) we calculated functional dispersion (FDis, Laliberté et al. 2010), estimated as the mean distance of all species to the weighted centroid of the community in the multivariate trait space (Anderson, Ellingsen, and McArdle 2006). In addition to quantifying the FDis to test for trait convergence at the bridge, we used the community weighted mean (CWM) of species traits, EiV and DiV to test for the dominance of species with a specific life span, native and invasive status and for the dominance of specific EiV and DiV at the bridge. CWM represents, for each indicator variable, the central tendency of the species traits in the community. For dispersal mode, we only used the CWMs of wind and water-dispersed species as these should be more representative of riverine and roadside habitats (Von Der Lippe and Kowarik 2007; Nilsson et al. 2010). We used the R package “FD” (Laliberté and Legendre 2015) in R statistical environment (R Core Team 2023) for all these calculations.

## 2.3 | Spatial Predictors

To represent overland spatial processes without directionality constraints, we constructed spatial eigenvectors using Moran's Eigenvector Maps method (MEM; Dray, Legendre, and Peres-Neto 2006). MEM consists of the double-diagonalisation of a spatial weighting matrix generated from the quadrats' geographical location. We optimized the selection of a spatial weighting matrix and of a subset of spatial predictors following recommendations of Bauman, Drouet, Fortin, and Dray (2018), Bauman, Drouet, Dray, and Vleminckx (2018).

To represent directional watercourse spatial processes, we constructed Asymmetric Eigenvector Maps (AEM, Blanchet, Legendre, and Borcard 2008), a modified version of MEM aimed

at accounting for directionality in the connectivity among quadrats. In our case, AEMs considered inland distances following the water and road courses. In AEM, building the connectivity matrix to define the connection between two samples is usually done based on their geographic coordinates using the `aem.build.binary()` (“*adespatial*” package; Dray et al. 2021). To handle complex spatial networks without relying on the geographic coordinates to connect samples, instead, we used the `nodes_by_edges_matrix()` function (“*chessboard*” package, built *ad hoc* for this study; Casajus et al. 2023). This function connects samples only based on node labels, that is, considering the numeric order of node labels to give the dimension and the direction of the network (the first node is the most upstream and the last is most downstream). This method allows the representation of the river channel sinuosity to create the watercourse connections among quadrats. Due to the complexity of our study design to create the node labels, the network needed to be separated between the left and right margins of the river. We present here the results of the left margin network, but the results of the right margin were comparable (Table S2).

## 2.4 | Data Analysis

(1) Are the alpha and beta diversities of plant communities affected by bridges?

To investigate the effect of bridges on alpha diversity of quadrats (richness and Shannon index) and on beta diversity among quadrats (per block,  $\beta$ Block and per zone within each block  $\beta$ ZoneA,  $\beta$ ZoneB,  $\beta$ ZoneC), we used linear mixed effects (LME) models using the package “*lme4*” (Bates et al. 2015). We used “site” identity as a random effect to account for the non-independence of observations among blocks from the same site, and treatment (i.e., bridge and reference), corridor (i.e., road and river) and their interaction as the main fixed effects. We also included river systems (i.e., Adour or Garonne rivers) and zone (i.e., A, B and C) as additional fixed effects. Whenever zone was found to be significant, we constructed additional models with an interaction term between treatment and zone to investigate how each zone is affected by bridges. To account for the effect of climate, soil, environment and land cover that may structure plant community assemblages at bridges, we collected several environmental co-variables at the block level. Details on how each variable was extracted can be found in Appendix S1. All co-variables were standardized to have zero mean and unit standard deviation. We conducted a preselection of predictor variables to avoid multicollinearity by calculating pairwise Pearson correlations between the explanatory variables. For any pair of variables with an absolute correlation greater than 0.7, we removed the variable that had the lowest correlation with each response variable. (Figure S1). To avoid collinearities among the binary and categorical variables (see Table S1), we also checked the variance inflation factor (VIF, Dormann et al. 2013). This led us to keep only one interaction term in the models, the one between treatment (bridge and reference) and corridor (road and river). The following co-variables were retained in the models: distance to the bridge, cation exchange capacity, soil nitrogen content, precipitation, altitude, % agriculture and population density.

We constructed candidate models using all possible combinations of the variables and ranked them based on the model AIC. The presence of significant spatial autocorrelation in the residuals of all selected candidate models was tested and removed, if present, using MEM (Dray, Legendre, and Peres-Neto 2006) and “method = MIR” (minimize residual autocorrelation) in the `listw.candidates()` function from package “*adespatial*” (Dray et al. 2021; Bauman, Drouet, Fortin, and Dray 2018; Bauman, Drouet, Dray, and Vleminckx 2018). This step is important to account for all possible residual spatial autocorrelation in different scales (regardless of the random error structures) as it avoids any statistical artifact from our complex sampling design. Once a subset of spatial predictors was selected to remove residual spatial autocorrelation from the initial model, the model was rerun with the additional spatial predictors, yielding unbiased coefficients for the ecological variables of interest. The first equally plausible candidate models (i.e.,  $\Delta AIC \leq 2$  and weight  $> 0.7$ , see Appendix S2) were averaged to address the uncertainty in the selection of the best candidate variables (Burnham, Anderson, and Huyvaert 2011) and estimates are reported based on full averages. Tukey HSD post hoc pairwise comparisons were performed between each level of treatment (bridge and reference) by corridor (road and river) using the package “*emmeans*” (Lenth et al. 2020). Model averaging could not be performed when the top subset of models only contained one model. In these cases, estimates for the top model are reported (Table S3). These analyses were done in the “*MuMIn*” package (Barton 2016).

(2) Do environmental filters at bridges favor species with similar ecological preferences, leading to trait convergence, compared to plant communities on river and road sides away from bridges?

We assessed the effect of bridges on FDis and on CWMs of species traits (i.e., lifespan, dispersal mode, and native and invasive status), EiV and DiV with LME models, with “site” as a random effect, and “treatment” (i.e., bridge and reference), “corridor” (i.e., road and river) and their interaction as main fixed effects. We were particularly interested in the interaction term to test whether plant communities of roads and rivers converged at bridges toward the same specific ecological strategies. In all models we also included “river system” (i.e., Adour and Garonne) and “zone” (i.e., A, B and C) as fixed effects, and environmental and spatial predictors as co-variables, following all the same model selection procedures described in the Section 2.3. However, as the relationship between CWM values and sample attributes (e.g., environmental co-variables) has inflated type I error rates (Zelený and Schaffers 2012; Peres-Neto et al. 2017), for each model where a quantitative co-variable showed a significant effect, we additionally tested their significances with the “`test_cwm()`” function in the “*weimeia*” package (Zelený and Schaffers 2012). After this analysis, none of the co-variables were statistically significant in explaining CWM values and therefore were not further considered in the analysis (Table S4). For the FDis models, to remove the effect of species richness on FDis, we tested additional models using the model residuals of the regression of FDis on species richness and obtained similar effects (Tables S5 and S6).

(3) Are directional spatial processes more important than non-directional spatial processes in structuring riverside and

roadside species composition, and do bridges influence the effect of directional spatial predictors on species composition?

We used redundancy analysis (RDA) to estimate the respective contribution of Moran's Eigenvector Maps (MEM) and Asymmetric Eigenvector Maps (AEM)' spatial predictors on the species composition of plant communities. As response matrices, we used species' abundance data after Hellinger transformation and excluded 58 species occurring in only one sampling site. We then generated three sets of spatial predictors to explain species composition of the road-river metacommunity: (1) subset of optimized MEM spatial predictors, representing non-directional overland predictors, (2) AEM representing directional upstream-downstream water course predictors considering the connection between rivers and roads through the bridge, and (3) another AEM representing directional upstream-downstream water course predictors but without considering the connections between rivers and roads through the bridge. To construct the AEM, we considered the unidirectional upstream-downstream connection of quadrats along the river network and bidirectional connections of quadrats along the roads as all studied roads have traffic in both directions. For MEM models, we maximized the adjusted R-squared ( $R^2$ ) using "method = global" in the `mem.select()` function ("adespatial" package). For both MEM and AEM, we then used a forward selection with double stopping criterion (package 'vegan', Oksanen et al. 2020), as well as a third criterion to only continue the variable selection as long as select spatial predictors explained added at least 0.01 to the  $R^2$ . The models with and without the bridge connections allowed us to test if bridges influence the response of plant communities to directional spatial predictors. The two rivers were treated independently of each other (no connection between them). We also generated MEM and AEM only for the riverside community samples. We did not generate AEM only for the roadside community as our dataset contain only two-way roads and hence have no main directionality. Moreover, the sensitivity of AEM analysis based solely on bidirectional flows without one main directionality is unclear (Blanchet et al. 2011). For all spatial predictors, only positive eigenvectors, reflecting positive spatial autocorrelation patterns, were retained. For the AEM, this was determined by calculating Moran's I statistic and selecting only the eigenvectors with I statistic greater than that expected by

chance using the function `moran.randtest()` ("adespatial" package, Dray et al. 2021).

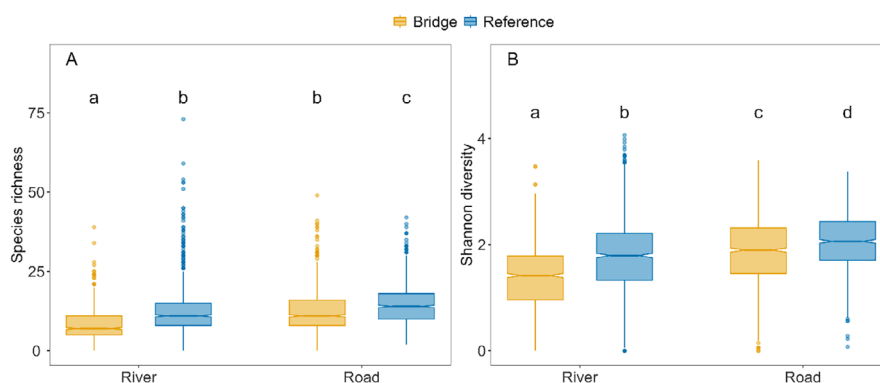
The overall statistical significance of the RDA models was evaluated by permutation tests using 9999 randomisations (Peres-Neto et al. 2006). The three sets of spatial predictors (i.e., MEM non-directional overland predictors, AEM directional upstream-downstream water course predictors: with or without bridge connections) were then contrasted based on the adjusted  $R^2$  produced by the RDA. The analyses were performed using the R statistical environment (R Core Team 2023). Figures were built using the "ggplot2" package (Wickham and Chang 2016).

### 3 | Results

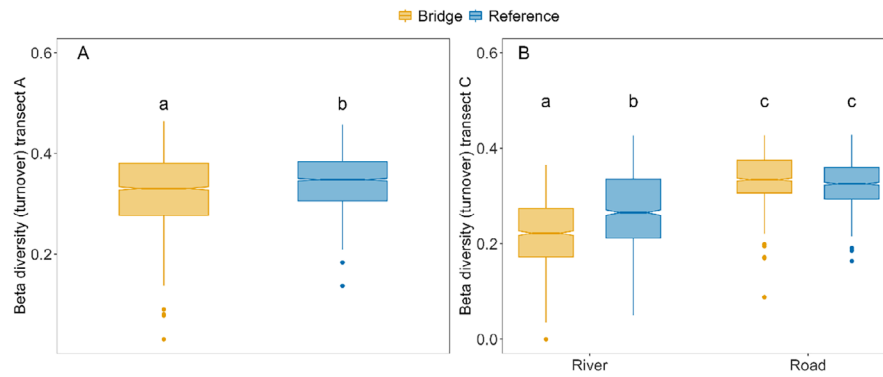
#### (1) Are the alpha and beta diversities affected by bridges?

Across the 4560 quadrats in our study area, we identified a total of 1446 species, with 1057 occurring at bridges, and 1299 at reference sites. Along rivers, we found 1093 species while 1139 species were found on roads. On rivers, we found on average 10 species per quadrat (ranging from 0 to 73), while on roads we found 13 species per quadrat (ranging from 0 to 49). Roads and rivers shared 786 species, with 353 species exclusive to roads and 307 species exclusive to rivers. Roads and rivers showed a similar percentage of native species on bridges (77% for both roads and rivers) and reference quadrats (78 and 79% for roads and rivers, respectively). Concerning invasive species, on roads, we found 0.5% and 0.6% of species on bridge and reference quadrats, respectively. Similar results were found for rivers (0.4% and 0.3% of invasive species on bridge and reference quadrats, respectively).

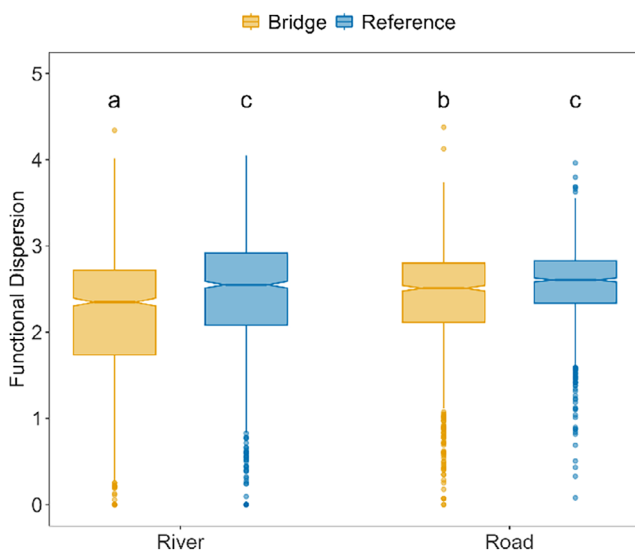
In rivers, mean species richness was ~33% higher in reference quadrats than in bridge quadrats (Figure 2A), except for zone C (further from the river channel, Figure S2). In roads, richness was also higher in reference quadrats (~16%, Figure 2A), except for zone A (Figure S2). Similar patterns were observed for Shannon's diversity with mean values ~15% higher on reference quadrats for rivers and ~12% higher on reference quadrats for roads (Figure 2B and Figure S2). Results from Tukey tests are shown in Table S6.



**FIGURE 2** | Bridge effect on species richness (A) and Shannon diversity (B) for rivers and roads. The center lines in boxes represent the medians of observed values; box limits indicate the 25th and 75th percentiles; whiskers extend 1.5 times the interquartile range from the 25th and 75th percentiles. Different lowercase letters indicate statistically significant differences in a pairwise comparison of least-squares means (Tukey HSD).



**FIGURE 3** | Bridge effect on the replacement component of beta diversity (turnover) per block. The interaction term between treatment (bridge vs. reference) and corridor (road vs. river) was not significant for transect A (panel A), therefore panel A displays the beta diversity for both roads and river together. The center lines in boxes represent the medians of observed values; box limits indicate the 25th and 75th percentiles; whiskers extend 1.5 times the interquartile range from the 25th and 75th percentiles. Different letters indicate statistically significant differences in a pairwise comparison of least-squares means (Tukey HSD).



**FIGURE 4** | Bridge effect on Functional Dispersion. The center lines in boxes represent the medians of observed values; box limits indicate the 25th and 75th percentiles; whiskers extend 1.5 times the interquartile range from the 25th and 75th percentiles. Different letters indicate statistically significant differences in a pairwise comparison of least-squares means (Tukey HSD).

Concerning beta diversity per block, we found a significant bridge influence only for the turnover component (replacement) in zones A ( $p = 0.002$ ) and C ( $p < 0.001$ ) (Figure 3, other results not shown because they are non-significant). Specifically, at the bridge, we observed lower turnover of species composition in comparison with reference blocks on roads and rivers for zone A (Figure 3A), and only on rivers for zone C (Figure 3B).

For roads only, quadrats at the bridge showed a higher percentage of annual species (Table S6). For both roads and rivers, there was no effect of bridges in the percentage of native and non-native species. Likewise, we did not find any differences between bridge and reference quadrats in the CWM of invasive vs. non-invasive status. For species dispersal mode no significant differences were found between bridge and reference (all results shown on Table S6).

**TABLE 1** | Proportion of variation (adjusted  $R^2$ ) in plant composition (left river and road sides) explained by the three spatial models for species composition.

	Adjusted $R^2$ (%)	
	Adour	Garonne
Unidirectional water course (AEM): river + road network connected by bridge	7.75	8.76
Unidirectional water course (AEM): river + road network not connected by bridge	6.39	7.17
Bidirectional overland (MEM): river + road network	17.46	21.24
Unidirectional water course (AEM): river network	13.33	12.78
Bidirectional overland (MEM): river network	30.75	32.85

Abbreviations: AEM, asymmetric eigenvector maps; MEM, Moran's eigenvector maps.

(2) Do environmental filters at bridges favor species with similar ecological preferences, leading to trait convergence, compared to plant communities on river and road sides away from bridges?

We found evidence for trait convergence of species ecological preferences in plant communities at bridges, as FDis was 13.2% lower on bridge quadrats compared to reference quadrats on rivers and 9.3% lower on roads (Figure 4—see Tables S5 and S6 for similar results when removing the effect of species richness on FDis). However, our results suggest that communities of roads and rivers did not converge toward the same ecological preferences at bridges, as the CWM mean values of EiV and DiV of roads were statistically different from those of rivers at bridge samples (Figure S3 and Table S6). Communities close to bridges on roads showed preferences for higher temperature EiV, lower air and soil moisture and lower organic matter, while on rivers, communities close to bridges showed preference for lower soil texture EiV (Figure S3). Regarding species' positions within



disturbance gradients, we found a significant increase in mean indicator value of species' response to soil physical disturbances (DiV) at bridges on roads (Figure S3). For all other EiV and DiV, we did not find significant differences between bridge and reference (Table S6).

(3) Are directional spatial processes more important than non-directional in structuring riverside and roadside species composition and do bridges influence directionality effects?

All sets of spatial predictors significantly explained the variation of the road-river metacommunity, and the percentage of explained variation was similar along the two rivers (Table 1). Models with and without bridge connections also explained similar amounts of variability (7.75 vs. 6.39%), with bridge connections not adding substantial difference to the results. Non-directional spatial predictors outperformed both AEM with higher explanatory power (17.46%). When assessed independently from roads, the effect of directional spatial predictors on riverside communities was also lower (AEM, 13.33%) than non-directional (MEM, 30.75%). Directional spatial predictors that best explained the spatial structures showed large scale spatial patterns (upstream-downstream water course and the latitudinal gradient), while directional spatial predictors related to fine scale structures showed differences between the roadside and riverside blocks and at the zone level (yellow and blue circles, Figure S4), but these were not observed consistently over all sites.

## 4 | Discussion

The aim of this study was to investigate the effect of bridges on the roadside and riverside plant communities and their role in driving species diversity and composition along two watersheds: the Adour and the Garonne. As expected, we found that the presence of a bridge has a significant local impact on species diversity, composition and ecological preferences. Specifically, quadrats at bridges exhibited lower plant richness and beta diversity for both rivers and roads compared to reference quadrats away from the bridge. We also found that proximity to bridges led to communities with species that converged in their ecological preferences, though not similarly in roads and rivers. Moreover, using an innovative combination of directional and non-directional spatial eigenfunction analyses, we showed that non-directional spatial predictors better describe the road-river metacommunity and found that, despite bridges having multiple effects on river-road plant communities, there is no evidence to support that the existence of bridges substantially affects directional spatial processes that drive plant species composition of road-river metacommunities. The practical implications of this study for management and conservation are that bridges, while not significantly affecting connectivity of the whole river and road network, have strong impacts on plant communities at the bridge itself, leading to reduced diversity and increased homogenization. These effects highlight the need for targeted management practices around bridge areas, such as reducing mowing frequency, preserving native vegetation, and minimizing habitat disturbance.

(1) Are species alpha and beta diversities of plant communities affected by bridges?

As expected, our results showed that bridges led to reduced species diversity. This might be due to unique characteristics of bridges and their management, such as vegetation mowing, albedo, presence of ripraps, etc. ("bridge effects" hereafter) that alter environmental filters. Compared to reference sites, bridges can impose environmental constraints that favor the dominance of species with certain ecological preferences, such as generalists and disturbance-tolerant species with high dispersal abilities (Olden et al. 2004; Bengtsson 2010) (see Section 2 below). Strong environmental constraints lead to community homogenization and reduced diversity, as many species are unable to persist under high levels of either stress or disturbance (McKinney 2006). Indeed, at bridges, we found more annual species on roads. Herben, Klimešová, and Chytrý (2018) reported an increase in annual species related to different types of disturbances (cutting, mowing, herbivory, trampling, application of herbicides, burning, wind-throws, soil erosion, flooding, etc.) and in different frequencies in several habitats in Central Europe. Annual species typically occupy the fresh open space after disturbance, even though they can later succumb to competition from long-lived species if the disturbance ceases (Herben, Klimešová, and Chytrý 2018).

At bridges, our results also showed reduced species beta diversity (turnover or replacement component) on the inner zone of road and river corridors and on the outer zone on rivers. The local similarity in species composition, that is decrease in the turnover component of beta diversity, also indicates biotic homogenization (Olden and Rooney 2006), and may be related to the bridge effects. Specifically, the inner zone is the most subject to environmental constraints whether for roads (more frequently mowed and closer to the steel-concrete composite pavement at bridges) or rivers (the most frequently flooded habitats closer to ripraps at bridges). It is possible that the intermediate zone (zone B) could eventually be flooded in reference and bridge conditions, leading to non-significant reduction in beta diversity at bridges. However, in the outer zone, it is likely that riverbank stabilization structures at bridges (riprap) reduce the width of the river channel and elevate the water level during floods (see Figure S5). Thus, the water could possibly reach the most external zone of the river corridor promoting a "flooding effect". During floods, water flow becomes the principal vector of diaspores within fluvial corridors and the main driver of the structure and composition of riparian plant communities (Tabacchi et al. 1998; Asaeda et al. 2011; Corenblit et al. 2016). This flooding effect near bridges can increase biological connectivity and the spread of organisms between locations that would not occur under baseflow conditions (Murphy et al. 2015). At higher dispersal rates, the metacommunity homogenizes due to increased colonization rates, resulting in losses of beta diversity (Mouquet and Loreau 2002). It is also likely that the outer zone on rivers is more frequently mowed to improve access for maintenance of bridges (see Figure S6), resulting in a physical homogenization of the habitat and in a reduction in species composition (due to a mix of disturbance and stress constraints).

(2) Do environmental filters at bridges favor species with similar ecological preferences, leading to trait convergence, compared to plant communities on river and road sides away from bridges?



As expected, functional trait values of co-occurring species were more similar close to bridges than in reference sites, indicating trait convergence within communities at bridges, despite the difference between bridge and reference in functional dispersion being small (13.2% lower on bridge quadrats compared to reference quadrats on rivers and 9.3% lower on roads). This finding shows that a smaller number of functional strategies were apparently preferred at bridges compared with reference sites. The bridge effects can lead to strong environmental constraints that filter a subset of organisms with similar functional trait values. In general, our results corroborate previous studies showing that the range of trait values within a community is expected to decrease with increasing environmental constraints (Cornwell, Schilck, and Ackerly 2006; Costa et al. 2017).

Bridges selected species with different strategies compared to reference sites on both rivers and roads, even though the significant differences captured by our models were small. However, our results also suggest that bridge effects impacted EiV and DiV differently on rivers compared to roads, and the communities of the two types of corridors did not converge toward the same strategy at bridges (Figure S3). On roads, communities at bridges showed preferences for lower organic matter, soil and air moisture, higher temperature and disturbed soils. Even though bridges should not represent a strong disruption of the roadside habitats' continuum (as compared to rivers), they require more severe practices for safety and maintenance, and their particular architecture imposes several sharp habitat changes such as drier and hotter pavement materials and thinner soil depth, in comparison to other road segments (Bonthoux et al. 2014; Mohajerani, Bakaric, and Jeffrey-Bailey 2017; Rosenfeld et al. 1995). Consistent with our findings indicating a higher percentage of annual species on roads at bridges, Midolo et al. (2023) also found that annual plants have an overall preference of disturbed soils. Our results also align with theoretical expectations that disturbance tends to favor annual and ruderal plants (Grime 1979). On rivers, communities close to bridges showed preferences for lower soil texture, that is, finer grain size. Excessive tillage or heavy machinery used to mow the vegetation on roads and around bridges (but not on riverside vegetation on reference sites) (Figure S6) can disrupt the soil structure and result in compaction, reducing soil texture (Batey 2009). Another possible explanation would be related to hydraulic turbulence close to the bridge causing fine sediment sorting (Bera et al. 2022).

(3) Are directional spatial processes more important than non-directional spatial processes in structuring riverside and roadside species composition, and do bridges influence the effect of directional spatial predictors on species composition?

Our findings indicate that directional spatial predictors derived from watercourse distances have lower explanatory power than overland non-directional spatial predictors in describing plant community composition of roadside and riverside vegetation. This suggests the lower importance of directional dispersal processes in comparison with non-directional spatially structured environmental characteristics. From an ecological point of view, a set of spatial variables derived from overland distances and selected as best predictors of community composition

represents climatic and environmental conditions, or non-directed dispersal limitation, whereas such a set of spatial variables derived from watercourse distances is more likely to mostly relate to dispersal processes within aquatic and riparian ecosystems or strongly dominant winds (Bourgeois et al. 2016). Here we also considered that anthropogenic structures could facilitate or disrupt the regional movement of propagules between community patches on a fragmented landscape, by analyzing two scenarios reflected by our connectivity matrices: one with bridges, and another without bridges connecting the road-river metacommunity.

Contrary to our expectations, overland non-directional spatial predictors (MEM) were more important than watercourse directional spatial predictors (AEM) even to explain riverside community composition. Whereas higher explanatory capacity of AEM for riverside plant communities was found in studies in smaller sampling areas in riverbanks in NE Canada (Bourgeois et al. 2016; Brice, Pellerin, and Poulin 2016), it is possible that directionality may have been masked by the high heterogeneity and higher diversity of our habitats (compared to the studies in NE Canada). Concerning the influence of bridges, the small difference in the proportion of variability explained by our two AEM models (with and without bridge connection) suggests that the existence of bridges does not substantially affect directional spatial process that drive plant species composition along the studied river systems, hence the connectivity between road and river vegetation.

## 5 | Conclusion

As expected, we found that the presence of a bridge has a significant impact on species diversity, composition and ecological preferences in road and river plant communities, even if this impact is low for some variables. Noteworthy, we found increased trait convergence at bridges compared to sites far from bridges. Yet, we did not find evidence that bridges strongly affect the species composition in the combined network for the whole watershed, at least for plant communities. Nevertheless, the strong effect of bridges as selecting forces of plant communities locally for both rivers and roads independently suggests bridges should not be neglected. By addressing the specific environmental filters created by bridges, land managers can mitigate the negative effects on species diversity and composition, ultimately helping to maintain ecosystem function and biodiversity in these fragmented landscapes. Here we considered realized metrics of metacommunity structure as proxy of biological connectivity. We suggest that future studies consider more appropriate descriptors such as diaspore dispersion and gene fluxes to better demonstrate processes related to ecological connectivity.

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## Conflicts of Interest

The authors declare no conflicts of interest.

## Data Availability Statement

The data that support the findings are available at <https://doi.org/10.5281/zenodo.14562208>.

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### Supporting Information

Additional supporting information can be found online in the Supporting Information section.