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1 **Road-river intersections (bridges) negatively affect plant species diversity and ecological attributes**

2 Erica Rievers Borges<sup>1,2\*</sup>, Eduardo González-Sargas<sup>3</sup>, Nicolas Casajus<sup>1</sup>, Marta Carboni<sup>4</sup>, David Bauman<sup>2</sup>,  
3 Guillaume Fried<sup>6</sup>, Lindsay Maskell<sup>7</sup>, Alejandro Juarez Escario<sup>8</sup>, Anne-Marie Planty-Tabacchi<sup>9</sup>, Eric  
4 Tabacchi<sup>9</sup>

5

6 <sup>1</sup> *FRB-CESAB, Montpellier, France.*

7 <sup>2</sup> *AMAP, Univ Montpellier, IRD, CNRS, CIRAD, INRA, Montpellier, France.*

8 <sup>3</sup> *Colorado State University, Department of Biology, Fort Collins, United States of America*

9 <sup>4</sup> *Department of Sciences, Università Roma TRE, Roma, Italy.*

10 <sup>5</sup> *ANSES, Laboratoire de la Santé des Végétaux, Unité Entomologie et Botanique, Montferrier-sur-Lez,*  
11 *France.*

12 <sup>6</sup> *UKCEH, Lancaster Environment centre, Lancaster Great Britain.*

13 <sup>7</sup> *Department of Agricultural and Forest Sciences and Engineering. University of Lleida, Lleida, Spain.*

14 <sup>8</sup> *Laboratoire Ecologie Fonctionnelle et Environnement, CNRS, Université Paul Sabatier, Institut National*  
15 *Polytechnique, Toulouse Cedex 9, France.*

16

17 **Abstract**

18

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

22 Location: Southern France

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

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

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

38  
39  
40 Key-words: riparian zones, corridor intersections, landscape fragmentation, spatial eigenvector maps,  
41 biodiversity, connectivity, urban ecosystems, linear habitats

## 43 **Introduction**

44  
45 Linear habitats consist of terrestrial and aquatic corridors, which can be natural such as hedgerows,  
46 grass strips and rivers or anthropogenic, like roads, railway lines and canals. These habitats are commonly  
47 considered in biodiversity and environmental management policies. For example, the European Blue-Green

48 Infrastructure policy (BGI, ‘green’ vegetation, and ‘blue’ water spaces) prioritises strategically planned  
49 networks where different linear habitats intersect to enhance connectivity and possibly biodiversity and  
50 ecosystem services (European Union Commission 2013). At the landscape scale, maintaining well-  
51 connected habitats to function as ecological corridors might be beneficial for biodiversity in the context of  
52 climate change, by facilitating species dispersal towards new suitable refuge areas, or acting as refugia  
53 themselves (Smart et al. 2006a; Smart et al. 2006b; Villemey et al. 2018). However, at local scales, a high  
54 degree of connectivity can be detrimental, due to the increased spread of invasive species (Glen et al. 2013),  
55 and, from a metacommunity perspective, beta diversity can also be negatively affected because high levels  
56 of dispersal can contribute to biotic homogenization (Mouquet and Loreau 2002). Although the importance  
57 of managing linear features at the landscape scale to optimize biodiversity is well recognized (Tiang et al.  
58 2021; Dilts et al. 2022), the role of intersections in enhancing or reducing connectivity among different  
59 linear corridors remains largely unexplored.

60 Rivers and roads are linear habitats of great ecological and social importance. Rivers supply  
61 multiple ecological functions and ecosystem services, such as nutrient, sediment, and water flow control,  
62 support for biodiversity and climate regulation (Tabacchi et al. 1998; Hood and Naiman 2000; Décamps  
63 2011). In parallel, most of the planet is fragmented by roads (Ibisch et al. 2016), and their extension is  
64 projected to increase by more than 60% from 2010 to 2050 (Dulac 2013). In contrast to river corridors, road  
65 corridors cause landscape fragmentation (Niu et al. 2018), with potentially negative consequences for  
66 biodiversity (Laurance and Vasconcelos 2009; Gardiner et al. 2018), carbon storage and water regulation  
67 (Molina et al. 2023). Yet, roads are also potential corridors for wildlife, in some cases hosting rare and  
68 threatened species (Gardiner et al. 2018; Wagner et al. 2019).

69 Rivers and roads intersect at bridges. Bridges can create specific environmental constraints that  
70 impact plant communities and species dispersal. Some constraints, such as the clearing of vegetation for  
71 safety and maintenance, which reduces local biomass affect both roads and rivers. In rivers, in addition to  
72 the presence of bridge piers, the installation of ripraps, which are protective barriers of rocks and concrete  
73 used to stabilize the river bank and secure the bridge foundation, may increase hydraulic turbulence and the

74 effects of flooding (Richardson et al. 2007; Vallet et al. 2010; Kowarik 2011; Reid and Church 2015). The  
75 steel-concrete composite pavement characteristic of bridges increases substrate and air temperature more  
76 than usually found along roads (Godefroid and Koedam 2007). These effects caused by bridges and their  
77 related environmental constraints can also promote further biotic homogenization of plant communities by  
78 filtering species with specific ecological preferences and reducing overall functional diversity (Cornwell et  
79 al. 2006; Costa et al. 2017). Because bridge effects could impact both roads and rivers, ecological traits of  
80 plant communities of these two types of habitats are expected to converge at bridges (Perry et al. 2018;  
81 Travers et al. 2021).

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

98           Plant community composition can be spatially structured by directional and non-directional spatial  
99 patterns. A directional upstream-to-downstream gradient is typically the main factor structuring riparian

100 plant communities because of its overarching influence on water, sediments, nutrient fluxes, and dispersal  
101 of propagules (Nilsson et al. 2010; Bourgeois et al. 2016). However, directional processes may not be as  
102 important in structuring plant communities along regulated and fragmented rivers, as the capacity of linear  
103 habitats to act as corridors of propagules depends on the distance an organism can travel between connected  
104 sites, but also on modifications to the river system (e.g., dams, culverts, channelization and bridges) (Ward  
105 and Stanford 1995; Nilsson et al., 2002; Aronson et al. 2016). Road corridors also disperse plants through  
106 vehicle movements (Von Der Lippe and Kowarik 2008; Lemke et al. 2018) and road maintenance activities  
107 (Christen and Matlack 2009), but these are not unidirectionally oriented when considering two-way roads.  
108 Dominant patterns of spatial variability can be studied with eigenvector maps (Blanchet et al. 2008, 2011),  
109 either when a directional forcing process is expected (Asymmetric Eigenvector Maps, AEM) or when no  
110 main directionality is hypothesized (Moran's Eigenvector Maps, MEM). However, to our knowledge, AEM  
111 has been used to investigate plant community composition along river systems (e.g., Bourgeois et al. 2016;  
112 Brice et al. 2016, Henry et al. 2018), but never along other terrestrial linear habitats or to understand the  
113 effect of road-river metacommunities.

114           With the construction of an increasing number of roads to fulfil rising transportation needs and  
115 considering the increasing vulnerability of riparian communities, it is, therefore, important to better unravel  
116 the effect of bridges on road and river plant communities. This understanding will inform more effective  
117 management of both types of linear habitats for the conservation of the plant species they host and the  
118 associated ecological functions and ecosystem services they provide. It can also help to develop more  
119 integrative, conjoining management policies, considering distinct corridor types and their interactions.  
120 Focusing on two river systems in southern France, we tested the response of diversity and ecological  
121 preferences to the bridge influence on the roadside and riverside vegetation, while controlling for climate,  
122 soil, environmental and land cover variables. More specifically, we asked: 1) Are the alpha and beta  
123 diversities of plant communities affected by bridges? 2) Do environmental filters at bridges favor species  
124 with similar ecological preferences, leading to trait convergence, compared to plant communities on river  
125 and roadsides away from bridges? And finally: 3) Are directional spatial processes more important than

126 non-directional spatial processes in structuring riverside and roadside species composition, and do bridges  
127 influence the effect of directional spatial predictors on species composition?

128

## 129 **Material and Methods**

### 130 **Study area and vegetation surveys**

131

132 The study area was the Adour-Garonne administrative basin (approx. 116,000 km<sup>2</sup>), which  
133 occupies most of the southwest of France (Figure 1). Both the Adour (approx. 330 km long, elevation  
134 gradient: 2876 m) and the Garonne (approx. 650 km, elevation gradient: 2360 m) rivers have their sources  
135 in the Pyrenees Mountain range (on the Spanish side for the Garonne), and flow in a NW direction through  
136 a very diverse territory including a wide elevational range towards their confluence with the Atlantic Ocean  
137 at the cities of Bayonne (Adour) and Bordeaux (Garonne), respectively. The road network in France contains  
138 over 1 million km and is the longest and one of the densest in the European Union (Ouédraogo et al. 2020).  
139 The sample design was built considering the following hierarchy, detailed below:  
140 site>block>zones>quadrats. We selected nine sites along the Adour River (AD01 to AD09) and ten sites  
141 along the Garonne River (GA01 to GA10) with approximately 30 km distance separating two consecutive  
142 sites along each river (Figure 1I). Each site was centered on a bridge, but we distinguished ‘bridge’ sampling  
143 locations on each corridor (road or river, 20 m apart from the bridge), and a ‘reference’ location,  
144 representative of the control locations along each corridor (1 to 2 km from the bridge structure). This set-up  
145 resulted in 16 sampling blocks per site: 8 on the roadside, and 8 on the riverside. Blocks were distributed on  
146 both sides upstream and downstream from the bridge along the river, and on both sides before and after the  
147 bridge along the road (see Figure 1II), totalling 304 blocks (19 sites x 16 blocks).

148 Three zones (or strips) were distinguished within each block: an internal (A), an intermediate (B)  
149 and an external zone (C; Figure 1III and IV). The internal zone (A) of roads corresponded to the vegetated  
150 part in contact with the asphalt roadway (i.e. berm). It is the most frequently mown, and therefore hosts only  
151 herbaceous species. For rivers, it corresponded to the most frequently flooded habitats, directly in contact

152 with the main water channel. Zone A of rivers can be colonized by herbaceous or shrubby vegetation, but  
153 also occupied by pioneer or late-successional tree vegetation. The intermediate zone (B) of roads may or  
154 may not include a drainage ditch. For the river, zone B was associated with a variety of habitats. The external  
155 zone (C) represented the edge between the linear habitats (road or river) and the surrounding landscape. For  
156 roads, it could host planted trees. For rivers, this edge marked the boundary with a riparian-terrestrial habitat.

157 At each zone of each block, we set up study transects that consisted of five quadrats of 2 x 0.5 m  
158 (1 m<sup>2</sup>) separated by 1.5 m. Transects within each zone run parallel to the corridor. In total, 4,560 quadrats  
159 were surveyed in the summer of 2015. For each of these quadrats, sampling consisted of the identification  
160 and the visual estimation of the relative cover of all plant species. Bare substrate cover was also recorded.  
161 Taxonomic nomenclature followed Flora Gallica (Tison and de Foucaud 2014).

162

### 163 **Plant community (response) variables**

164

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

173 In addition to these measures of taxonomic diversity, we also retrieved information on species 1)  
174 traits, 2) ecological preferences and 3) disturbance responses from several public databases. First, as species  
175 traits, we identified the life span of all species (short vs long-lived), and retrieved data on species dispersal  
176 modalities from the Baseflor database (Julve 2015). We also included species native (native vs non-native)  
177 and invasive (invasive vs non-invasive) status according to the French National Botanical Conservatory

178 (CBN) and regional lists (Caillon and Lavoué 2016; Cottaz and Dao 2021). Second, to describe species  
179 ecological preferences, we extracted Ellenberg's indicator values (EiV, Ellenberg et al. 1991) from the  
180 Baseflor database (Julve 2005). Ellenberg's indicator values are based on a simple ordinal classification of  
181 plants according to the position of their realized ecological niche along an environmental gradient. They  
182 give information about the performance of a plant in its realized niche and represent estimates of species  
183 ecological optima along the main ecological gradients. Specifically, we considered the following seven EiV  
184 related to environmental, climatic and substrate preferences: light, nutrient and soil moisture (resource  
185 availability), air moisture and temperature (climate), organic matter content and soil texture (soil properties).  
186 Third, we used indicator values of species' optimal positioning along disturbance gradients (see Midolo et  
187 al. 2023) based on their responses to mowing and soil physical disturbances (DiV).

188         We then quantified functional diversity using the EiV and DiV of species within each quadrat. To  
189 assess functional diversity and identify if species within quadrats responded similarly to environmental  
190 constraints (trait convergence) we calculated functional dispersion (FDis, Laliberté et al. 2010), estimated  
191 as the mean distance of all species to the weighted centroid of the community in the multivariate trait space  
192 (Anderson et al. 2006). In addition to quantifying the FDis to test for trait convergence at the bridge, we  
193 used the Community Weighted Mean (CWM) of species traits, EiV and DiV to test for the dominance of  
194 species with a specific life span, native and invasive status and for the dominance of specific EiV and DiV  
195 at the bridge. CWM represents, for each indicator variable, the central tendency of the species traits in the  
196 community. For dispersal mode, we only used the CWMs of wind and water-dispersed species as these  
197 should be more representative of riverine and roadside habitats (von der Lippe et al. 2007; Merritt et al.  
198 2010; Bjawa et al. 2018). We used the R package 'FD' (Laliberté and Legendre 2015) in R statistical  
199 environment (R Core Team 2023) for all these calculations.

200

## 201 **Spatial predictors**

202

203 To represent overland spatial processes without directionality constraints, we constructed spatial  
204 eigenvectors using Moran's Eigenvector Maps method (MEM; Dray et al. 2006). MEM consists of the  
205 double-diagonalisation of a spatial weighting matrix generated from the quadrats' geographical location.  
206 We optimised the selection of a spatial weighting matrix and of a subset of spatial predictors following  
207 recommendations of Bauman et al. (2018a,b).

208 To represent directional watercourse spatial processes, we constructed Asymmetric Eigenvector  
209 Maps (AEM, Blanchet et al. 2008), a modified version of MEM aimed at accounting for directionality in  
210 the connectivity among quadrats. In our case, AEMs considered inland distances following the water and  
211 road courses. In AEM, building the connectivity matrix to define the connection between two samples is  
212 usually done based on their geographic coordinates using the `aem.build.binary()` ('adespatial' package; Dray  
213 et al. 2021). To handle complex spatial networks without relying on the geographic coordinates to connect  
214 samples, instead, we used the `nodes_by_edges_matrix()` function ('chessboard' package, built *ad hoc* for  
215 this study; Casajus et al. 2023). This function connects samples only based on node labels, i.e., considering  
216 the numeric order of node labels to give the dimension and the direction of the network (the first node is the  
217 most upstream and the last is most downstream). This method allows the representation of the river channel  
218 sinuosity to create the watercourse connections among quadrats. Due to the complexity of our study design  
219 to create the node labels, the network needed to be separated between the left and right margins of the river.  
220 We present here the results of the left margin network, but the results of the right margin were comparable  
221 (Table A2).

222

## 223 **Data analysis**

224

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

226 To investigate the effect of bridges on alpha diversity of quadrats (richness and Shannon index)  
227 and on beta diversity among quadrats (per block,  $\beta$ Block and per zone within each block  $\beta$ ZoneA,  $\beta$ ZoneB,  
228  $\beta$ ZoneC), we used linear mixed effects (LME) models using the package 'lme4' (Bates et al. 2015). We

229 used 'site' identity as a random effect to account for the non-independence of observations among blocks  
230 from the same site, and treatment (i.e., bridge and reference), corridor (i.e. road and river) and their  
231 interaction as the main fixed effects. We also included river systems (i.e. Adour or Garonne rivers) and zone  
232 (i.e. A, B and C) as additional fixed effects. Whenever zone was found to be significant, we constructed  
233 additional models with an interaction term between treatment and zone to investigate how each zone is  
234 affected by bridges. To account for the effect of climate, soil, environment and land cover that may structure  
235 plant community assemblages at bridges, we collected several environmental co-variables at the block level.  
236 Details on how each variable was extracted can be found in Appendix 1. All co-variables were standardised  
237 to have zero mean and unit standard deviation. We conducted a preselection of predictor variables to avoid  
238 multicollinearity by calculating pairwise Pearson correlations between the explanatory variables. For any  
239 pair of variables with an absolute correlation greater than 0.7, we removed the variable that had the lowest  
240 correlation with each response variable. (Figure A1). To avoid collinearities among the binary and  
241 categorical variables (see Table A1), we also checked the variance inflation factor (VIF, Dormann et al.  
242 2013). This led us to keep only one interaction term in the models, the one between treatment (bridge and  
243 reference) and corridor (road and river). The following co-variables were retained in the models: distance  
244 to the bridge, cation exchange capacity, soil nitrogen content, precipitation, altitude, % agriculture and  
245 population density.

246 We constructed candidate models using all possible combinations of the variables and ranked them  
247 based on the model AIC. The presence of significant spatial autocorrelation in the residuals of all selected  
248 candidate models was tested and removed, if present, using MEM (Dray et al. 2006) and 'method=MIR'  
249 (minimize residual autocorrelation) in the listw.candidates() function from package 'adespatial' (Dray et al.  
250 2021; Bauman et al. 2018a,b). This step is important to account for all possible residual spatial  
251 autocorrelation in different scales (regardless of the random error structures) as it avoids any statistical  
252 artifact from our complex sampling design. Once a subset of spatial predictors was selected to remove  
253 residual spatial autocorrelation from the initial model, the model was rerun with the additional spatial  
254 predictors, yielding unbiased coefficients for the ecological variables of interest. The first equally plausible

255 candidate models (i.e.,  $\Delta AIC \leq 2$  and weight  $>0.7$ , see Appendix 2) were averaged to address the uncertainty  
256 in the selection of the best candidate variables (Burnham et al. 2011) and estimates are reported based on  
257 full averages. Tukey HSD post-hoc pairwise comparisons were performed between each level of treatment  
258 (bridge and reference) by corridor (road and river) using the package ‘emmeans’ (Lenth et al. 2020). Model  
259 averaging could not be performed when the top subset of models only contained one model. In these cases,  
260 estimates for the top model are reported (Table A3). These analyses were done in the ‘MuMIn’ package  
261 (Barton 2016).

262  
263 2) Do environmental filters at bridges favor species with similar ecological preferences, leading to trait  
264 convergence, compared to plant communities on river and road sides away from bridges?

265  
266 We assessed the effect of bridges on FDis and on CWMs of species traits (i.e. lifespan, dispersal  
267 mode, and native and invasive status), EiV and DiV with LME models, with ‘site’ as a random effect, and  
268 ‘treatment’ (i.e. bridge and reference), ‘corridor’ (i.e. road and river) and their interaction as main fixed  
269 effects. We were particularly interested in the interaction term to test whether plant communities of roads  
270 and rivers converged at bridges towards the same specific ecological strategies. In all models we also  
271 included ‘river system’ (i.e., Adour and Garonne) and ‘zone’ (i.e., A, B and C) as fixed effects, and  
272 environmental and spatial predictors as co-variables, following all the same model selection procedures  
273 described in the previous section. However, as the relationship between CWM values and sample attributes  
274 (e.g. environmental co-variables) has inflated type I error rates (Zelený and Schaffers 2012; Peres-Neto et  
275 al. 2017), for each model where a quantitative co-variable showed a significant effect, we additionally tested  
276 their significances with the ‘test\_cwm()’ function in the ‘weimea’ package (Zelený and Schaffers 2012).  
277 After this analysis, none of the co-variables were statistically significant in explaining CWM values and  
278 therefore were not further considered in the analysis (Table A4). For the FDis models, to remove the effect  
279 of species richness on FDis, we tested additional models using the model residuals of the regression of FDis  
280 on species richness and obtained similar effects (Table A5 and A6).

281  
282 3) Are directional spatial processes more important than non-directional spatial processes in structuring  
283 riverside and roadside species composition, and do bridges influence the effect of directional spatial  
284 predictors on species composition?

285  
286 We used redundancy analysis (RDA) to estimate the respective contribution of Moran's  
287 Eigenvector Maps (MEM) and Asymmetric Eigenvector Maps (AEM)' spatial predictors on the species  
288 composition of plant communities. As response matrices, we used species' abundance data after Hellinger  
289 transformation and excluded 58 species occurring in only one sampling site. We then generated three sets  
290 of spatial predictors to explain species composition of the road-river metacommunity: 1) subset of optimised  
291 MEM spatial predictors, representing non-directional overland predictors, 2) AEM representing directional  
292 upstream-downstream water course predictors considering the connection between rivers and roads through  
293 the bridge, and 3) another AEM representing directional upstream-downstream water course predictors but  
294 without considering the connections between rivers and roads through the bridge. To construct the AEM,  
295 we considered the unidirectional upstream-downstream connection of quadrats along the river network and  
296 bidirectional connections of quadrats along the roads as all studied roads have traffic in both directions. For  
297 MEM models, we maximized the adjusted R-squared ( $R^2$ ) using 'method=global' in the mem.select()  
298 function ('adespatial' package). For both MEM and AEM, we then used a forward selection with double  
299 stopping criterion (package 'vegan', Oksanen 2020), as well as a third criterion to only continue the variable  
300 selection as long as select spatial predictors explained added at least 0.01 to the  $R^2$ . The models with and  
301 without the bridge connections allowed us to test if bridges influence the response of plant communities to  
302 directional spatial predictors. The two rivers were treated independently of each other (no connection  
303 between them). We also generated MEM and AEM only for the riverside community samples. We did not  
304 generate AEM only for the roadside community as our dataset contain only two-way roads and hence have  
305 no main directionality. Moreover, the sensitivity of AEM analysis based solely on bidirectional flows  
306 without one main directionality is unclear (Blanchet et al. 2011). For all spatial predictors, only positive

307 eigenvectors, reflecting positive spatial autocorrelation patterns, were retained. For the AEM, this was  
308 determined by calculating Moran's I statistic and selecting only the eigenvectors with I statistic greater than  
309 that expected by chance using the function `moran.randtest()` ('adespatial' package, Dray et al. 2021).

310 The overall statistical significance of the RDA models was evaluated by permutation tests using  
311 9,999 randomisations (Peres-Neto et al. 2006). The three sets of spatial predictors (i.e., MEM non-  
312 directional overland predictors, AEM directional upstream-downstream water course predictors: with or  
313 without bridge connections) were then contrasted based on the adjusted  $R^2$  produced by the RDA. The  
314 analyses were performed using the R statistical environment (R Core Team 2023). Figures were built using  
315 the 'ggplot2' package (Wickham and Chang 2016).

316

## 317 **Results**

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

319 Across the 4,560 quadrats in our study area, we identified a total of 1,446 species, with 1,057  
320 occurring at bridges, and 1,299 at reference sites. Along rivers, we found 1,093 species while 1,139 species  
321 were found on roads. On rivers, we found on average 10 species per quadrat (ranging from 0 to 73), while  
322 on roads we found 13 species per quadrat (ranging from 0 to 49). Roads and rivers shared 786 species, with  
323 353 species exclusive to roads and 307 species exclusive to rivers. Roads and rivers showed a similar  
324 percentage of native species on bridges (77% for both roads and rivers) and reference quadrats (78 and 79%  
325 for roads and rivers, respectively). Concerning invasive species, on roads, we found 0.5% and 0.6% of  
326 species on bridge and reference quadrats, respectively. Similar results were found for rivers (0.4% and 0.3%  
327 of invasive species on bridge and reference quadrats, respectively).

328 In rivers, mean species richness was ~33% higher in reference quadrats than in bridge quadrats  
329 (Figure 2A), except for zone C (further from the river channel, Figure A2). In roads, richness was also higher  
330 in reference quadrats (~16%, Figure 2A), except for zone A (Figure A2). Similar patterns were observed for

331 Shannon's diversity with mean values ~15% higher on reference quadrats for rivers and ~12% higher on  
332 reference quadrats for roads (Figure 2B and Figure A2). Results from Tukey tests are shown in Table A6).

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

338           For roads only, quadrats at the bridge showed a higher percentage of annual species (Table A6). For  
339 both roads and rivers, there was no effect of bridges in the percentage of native and non-native species.  
340 Likewise, we did not find any differences between bridge and reference quadrats in the CWM of invasive  
341 vs non-invasive status. For species dispersal mode no significant differences were found between bridge  
342 and reference (all results shown on Table A6).

343  
344 2) Do environmental filters at bridges favor species with similar ecological preferences, leading to trait  
345 convergence, compared to plant communities on river and road sides away from bridges?

346  
347           We found evidence for trait convergence of species ecological preferences in plant communities at  
348 bridges, as FDis was 13.2% lower on bridge quadrats compared to reference quadrats on rivers and 9.3%  
349 lower on roads (Figure 4 – see Table A5 and A6 for similar results when removing the effect of species  
350 richness on FDis). However, our results suggest that communities of roads and rivers did not converge  
351 towards the same ecological preferences at bridges, as the CWM mean values of EiV and DiV of roads were  
352 statistically different from those of rivers at bridge samples (Figure A3, Table A6). Communities close to  
353 bridges on roads showed preferences for higher temperature EiV, lower air and soil moisture and lower  
354 organic matter, while on rivers, communities close to bridges showed preference for lower soil texture EiV  
355 (Figure A3). Regarding species' positions within disturbance gradients, we found a significant increase in  
356 mean indicator value of species' response to soil physical disturbances (DiV) at bridges on roads (Figure

357 A3). For all other EiV and DiV, we did not find significant differences between bridge and reference (Table  
358 A6).

359  
360 3) Are directional spatial processes more important than non-directional in structuring riverside and roadside  
361 species composition and do bridges influence directionality effects?

362  
363 All sets of spatial predictors significantly explained the variation of the road-river metacommunity,  
364 and the percentage of explained variation was similar along the two rivers (Table 1). Models with and  
365 without bridge connections also explained similar amounts of variability (7.75 vs 6.39%), with bridge  
366 connections not adding substantial difference to the results. Non-directional spatial predictors outperformed  
367 both AEM with higher explanatory power (17.46%). When assessed independently from roads, the effect  
368 of directional spatial predictors on riverside communities was also lower (AEM, 13.33%) than non-  
369 directional (MEM, 30.75%). Directional spatial predictors that best explained the spatial structures showed  
370 large scale spatial patterns (upstream-downstream water course and the latitudinal gradient), while  
371 directional spatial predictors related to fine scale structures showed differences between the roadside and  
372 riverside blocks and at the zone level (yellow and blue circles, Figure A4), but these were not observed  
373 consistently over all sites.

374  
375 **Discussion**

376 The aim of this study was to investigate the effect of bridges on the roadside and riverside plant communities  
377 and their role in driving species diversity and composition along two watersheds: the Adour and the  
378 Garonne. As expected, we found that the presence of a bridge has a significant local impact on species  
379 diversity, composition and ecological preferences. Specifically, quadrats at bridges exhibited lower plant  
380 richness and beta diversity for both rivers and roads compared to reference quadrats away from the bridge.  
381 We also found that proximity to bridges led to communities with species that converged in their ecological

382 preferences, though not similarly in roads and rivers. Moreover, using an innovative combination of  
383 directional and non-directional spatial eigenfunction analyses, we showed that non-directional spatial  
384 predictors better describe the road-river metacommunity and found that, despite bridges having multiple  
385 effects on river-road plant communities, there is no evidence to support that the existence of bridges  
386 substantially affects directional spatial processes that drive plant species composition of road-river  
387 metacommunities. The practical implications of this study for management and conservation are that  
388 bridges, while not significantly affecting connectivity of the whole river and road network, have strong  
389 impacts on plant communities at the bridge itself, leading to reduced diversity and increased  
390 homogenization. These effects highlight the need for targeted management practices around bridge areas,  
391 such as reducing mowing frequency, preserving native vegetation, and minimizing habitat disturbance.

392

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

394 As expected, our results showed that bridges led to reduced species diversity. This might be due  
395 to unique characteristics of bridges and their management, such as vegetation mowing, albedo, presence of  
396 ripraps, etc (“bridge effects” hereafter) that alter environmental filters. Compared to reference sites, bridges  
397 can impose environmental constraints that favor the dominance of species with certain ecological  
398 preferences, such as generalists and disturbance-tolerant species with high dispersal abilities (Olden et al.  
399 2004; Bengtsson 2010) (see section 2 below). Strong environmental constraints lead to community  
400 homogenization and reduced diversity, as many species are unable to persist under high levels of either  
401 stress or disturbance (McKinney 2006). Indeed, at bridges, we found more annual species on roads. Herben  
402 et al. (2018) reported an increase in annual species related to different types of disturbances (cutting,  
403 mowing, herbivory, trampling, application of herbicides, burning, wind-throws, soil erosion, flooding, etc)  
404 and in different frequencies in several habitats in Central Europe. Annual species typically occupy the fresh  
405 open space after disturbance, even though they can later succumb to competition from long-lived species if  
406 the disturbance ceases (Herben et al. 2018).

407           At bridges, our results also showed reduced species beta diversity (turnover or replacement  
408 component) on the inner zone of road and river corridors and on the outer zone on rivers. The local similarity  
409 in species composition, i.e., decrease in the turnover component of beta diversity, also indicates biotic  
410 homogenization (Olden and Rooney 2006), and may be related to the bridge effects. Specifically, the inner  
411 zone is the most subject to environmental constraints whether for roads (more frequently mowed and closer  
412 to the steel-concrete composite pavement at bridges) or rivers (the most frequently flooded habitats closer  
413 to ripraps at bridges). It is possible that the intermediate zone (zone B) could eventually be flooded in  
414 reference and bridge conditions, leading to non-significant reduction in beta diversity at bridges. However,  
415 in the outer zone, it is likely that riverbank stabilization structures at bridges (riprap) reduce the width of the  
416 river channel and elevate the water level during floods (see Figure A5). Thus, the water could possibly reach  
417 the most external zone of the river corridor promoting a “flooding effect”. During floods, water flow  
418 becomes the principal vector of diaspores within fluvial corridors and the main driver of the structure and  
419 composition of riparian plant communities (Tabacchi et al. 1998; Asaeda et al. 2011; Corenblit et al. 2016).  
420 This flooding effect near bridges can increase biological connectivity and the spread of organisms between  
421 locations that would not occur under baseflow conditions (Murphy et al. 2015). At higher dispersal rates,  
422 the metacommunity homogenises due to increased colonisation rates, resulting in losses of beta diversity  
423 (Mouquet and Loreau 2002). It is also likely that the outer zone on rivers is more frequently mowed to  
424 improve access for maintenance of bridges (see Figure A6), resulting in a physical homogenization of the  
425 habitat and in a reduction in species composition (due to a mix of disturbance and stress constraints).

426  
427 2) Do environmental filters at bridges favor species with similar ecological preferences, leading to trait  
428 convergence, compared to plant communities on river and road sides away from bridges?

429           As expected, functional trait values of co-occurring species were more similar close to bridges than  
430 in reference sites, indicating trait convergence within communities at bridges, despite the difference between  
431 bridge and reference in functional dispersion being small (13.2% lower on bridge quadrats compared to  
432 reference quadrats on rivers and 9.3% lower on roads). This finding shows that a smaller number of

433 functional strategies were apparently preferred at bridges compared with reference sites. The bridge effects  
434 can lead to strong environmental constraints that filter a subset of organisms with similar functional trait  
435 values. In general, our results corroborate previous studies showing that the range of trait values within a  
436 community is expected to decrease with increasing environmental constraints (Cornwell et al. 2006; Costa  
437 et al. 2017).

438           Bridges selected species with different strategies compared to reference sites on both rivers and  
439 roads, even though the significant differences captured by our models were small. However, our results also  
440 suggest that bridge effects impacted EiV and DiV differently on rivers compared to roads, and the  
441 communities of the two types of corridors did not converge towards the same strategy at bridges (Figure  
442 A3). On roads, communities at bridges showed preferences for lower organic matter, soil and air moisture,  
443 higher temperature and disturbed soils. Even though bridges should not represent a strong disruption of the  
444 roadside habitats' continuum (as compared to rivers), they require more severe practices for safety and  
445 maintenance, and their particular architecture imposes several sharp habitat changes such as drier and hotter  
446 pavement materials and thinner soil depth, in comparison to other road segments (Bonthoux et al. 2014;  
447 Mohajerani et al. 2017; Rosenfeld et al. 1995). Consistent with our findings indicating a higher percentage  
448 of annual species on roads at bridges, Midolo et al (2023) also found that annual plants have an overall  
449 preference of disturbed soils. Our results also align with theoretical expectations that disturbance tends to  
450 favor annual and ruderal plants (Grime 1979). On rivers, communities close to bridges showed preferences  
451 for lower soil texture, i.e., finer grain size. Excessive tillage or heavy machinery used to mow the vegetation  
452 on roads and around bridges (but not on riverside vegetation on reference sites) (Figure A6) can disrupt the  
453 soil structure and result in compaction, reducing soil texture (Batey 2009). Another possible explanation  
454 would be related to hydraulic turbulence close to the bridge causing fine sediment sorting (Bera et al. 2022).

455  
456 3) Are directional spatial processes more important than non-directional spatial processes in structuring  
457 riverside and roadside species composition, and do bridges influence the effect of directional spatial  
458 predictors on species composition?

459 Our findings indicate that directional spatial predictors derived from watercourse distances have  
460 lower explanatory power than overland non-directional spatial predictors in describing plant community  
461 composition of roadside and riverside vegetation. This suggests the lower importance of directional  
462 dispersal processes in comparison with non-directional spatially structured environmental characteristics.  
463 From an ecological point of view, a set of spatial variables derived from overland distances and selected as  
464 best predictors of community composition represents climatic and environmental conditions, or non-  
465 directed dispersal limitation, whereas such a set of spatial variables derived from watercourse distances is  
466 more likely to mostly relate to dispersal processes within aquatic and riparian ecosystems or strongly  
467 dominant winds (Bourgeois et al. 2016). Here we also considered that anthropogenic structures could  
468 facilitate or disrupt the regional movement of propagules between community patches on a fragmented  
469 landscape, by analysing two scenarios reflected by our connectivity matrices: one with bridges, and another  
470 without bridges connecting the road-river metacommunity.

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

481

482 **Conclusion**

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

495

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501

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505

506

507 **Data availability statement**

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

509

510

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751 List of Appendices

752 Appendix 1. Environmental co-variables, supplementary details from statistical analysis, tables (A1 – A6),  
753 figures and photos (A1 – A6).

754 Appendix 2. Set of models generated by multimodel selection procedure within  $\Delta AICc \leq 2$ .

755 Appendix 3. The data set described in this article.

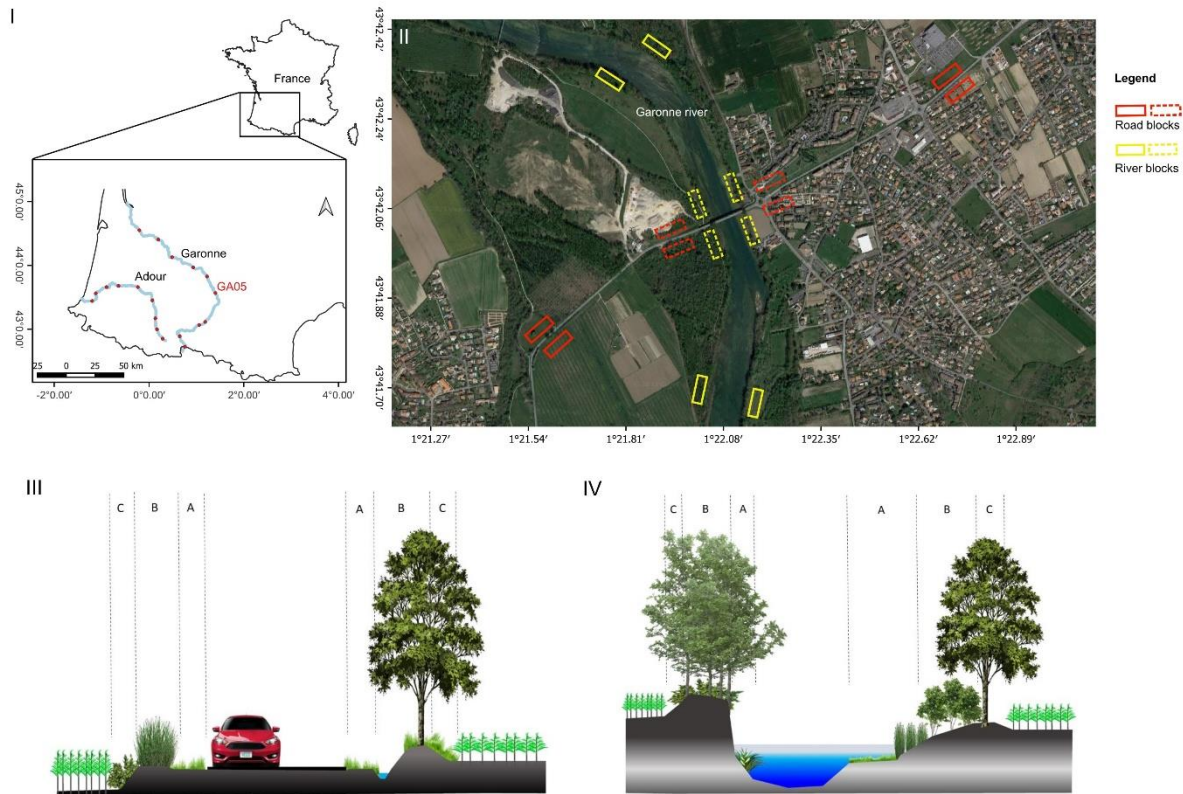
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757 **Figures**

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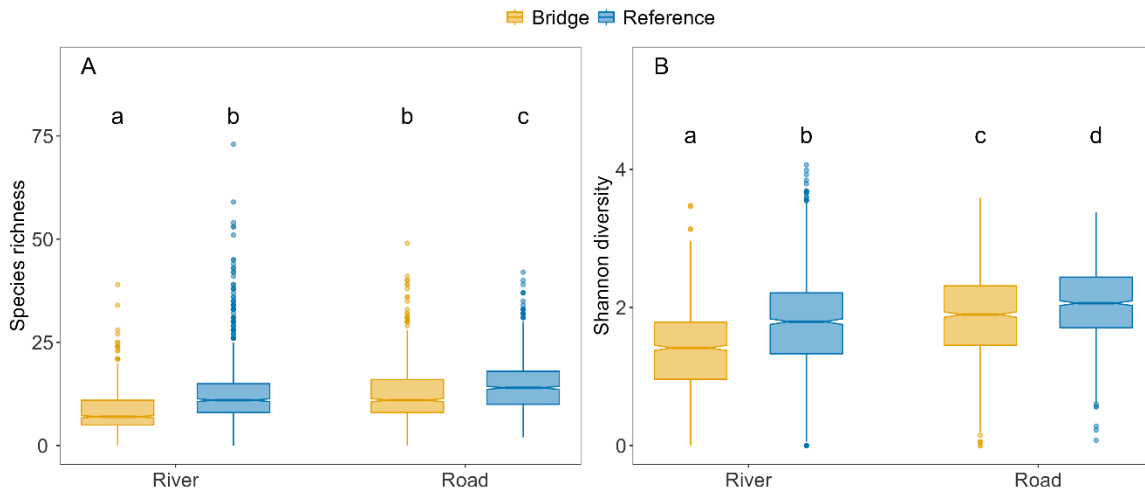


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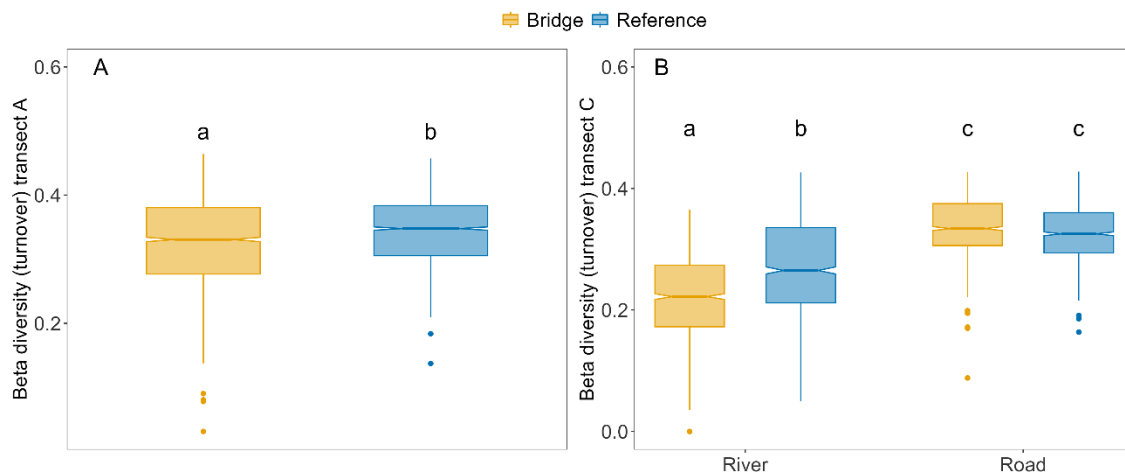
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763 Figure 1 Overview of the study sites illustrating: (I) sample area in the southwest of France and the location  
 764 of the 19 sample sites along the Adour and the Garonne rivers, (II) location of the river and road blocks by  
 765 the bridge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

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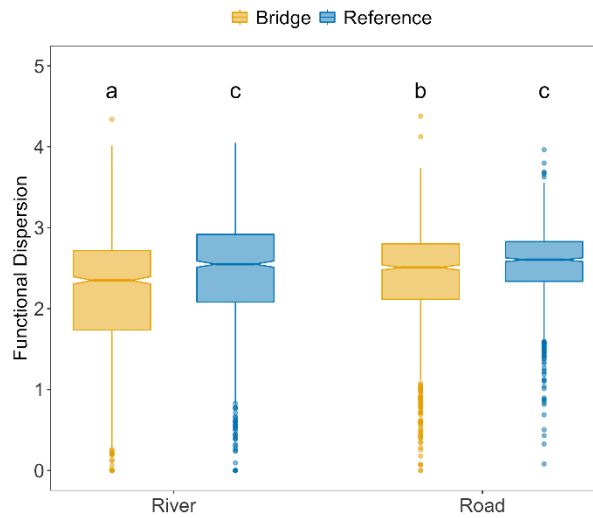


771  
 772 Figure 2. Bridge effect on species richness (A) and Shannon diversity (B) for rivers and roads. The center  
 773 lines in boxes represent the medians of observed values; box limits indicate the 25th and 75th percentiles;  
 774 whiskers extend 1.5 times the interquartile range from the 25th and 75th percentiles. Different lowercase  
 775 letters indicate statistically significant differences in a pairwise comparison of least-squares means (Tukey  
 776 HSD).  
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778  
 779 Figure 3. Bridge effect on the replacement component of beta diversity (turnover) per block. The interaction  
 780 term between treatment (bridge vs reference) and corridor (road vs river) was not significant for transect A  
 781 (panel A), therefore panel A displays the beta diversity for both roads and river together. The center lines in  
 782 boxes represent the medians of observed values; box limits indicate the 25th and 75th percentiles; whiskers

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