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1 **Riparian habitat connectivity restoration in an anthropized landscape: a multi-species approach**
2 **based on landscape graph and soil bioengineering structures**

3

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28 **Abstract**

29 In urbanized areas, rivers and riparian ecosystems are often the only ecological corridors available for
30 wildlife movement. There, riverbanks are often protected by civil engineering structures (dykes,
31 riprap). This can lead to habitat degradation and loss of landscape connectivity. Fascines (willow
32 bundles tied together) could be an alternative to riprap, since they maintain the quality of the natural
33 ecosystems by using native vegetal species instead of rocks, but their potential positive impact needs
34 to be assessed.

35 We proposed a landscape-scale decision-making method for river managers who want to restore banks
36 by transforming riprap into fascines to improve landscape connectivity. We applied our methodology
37 to a case study involving a 25km-stretch of the Arve river, France. We selected four target vertebrate
38 species based on biological traits to cover a wide range of dispersal capacities. For each species, we
39 used landscape graphs to assess habitat connectivity under different contrasted riverbank scenarios.
40 Scenarios included replacing all natural banks with ripraps or replacing all ripraps with fascines. In
41 addition, we systematically tested the effect of replacing individual 100 or 500m sections of ripraps by
42 fascines, to locate where riverbank restoration would maximize connectivity gain.

43 The four species selected responded very differently to the scenarios (up to +14% and +46% change in
44 Probability of Connectivity for common toads and Eurasian beavers, respectively, 0% for common
45 sandpipers and barred grass snakes). The restoration of specific riverbank sections could result in
46 important gains in PC (up to +33% for one single section for one species) but no section maximized
47 connectivity gain for all the target species.

48

49 **Keywords**

50 Ecological connectivity restoration, graph theory, riverbank, riverine landscape management,
51 vertebrates

52 **Introduction**

53 Riparian habitats are transition areas, or ecotones, at the interface between terrestrial and aquatic
54 habitats. They offer habitat to a wide variety of animal species, whether aquatic (e.g. for spawning and
55 nursery of juvenile fish (Mouton et al., 2012)), terrestrial (such as forest species), or dependent on
56 these specific environments (e.g. beaver). Riparian habitats are also crucial for connectivity across
57 these different types of environments for amphibious species, whose life cycles require both terrestrial
58 and aquatic habitats (Wells, 2007). These habitats are therefore of disproportionate ecological
59 importance in relation to their size as they are often only a few dozen metres wide (Sabo et al., 2005;
60 González et al., 2017; Hunter, 2017). The specific linear nature of rivers makes them potential biological
61 corridors, particularly in human-modified landscapes (Naiman et al., 1993; Erős et al., 2011; de la
62 Fuente et al., 2018). Biological corridors are areas that allow organisms to move through a landscape.
63 In particular, they enable gene flow, which is of great importance for biodiversity conservation. Their
64 conservation is often integrated into public environmental policies (Rosenberg et al., 1997; Van Der
65 Windt & Swart, 2007).

66 Under natural conditions, rivers and riparian zones are highly dynamic systems changing their position
67 and extensions in the landscape following hydrogeomorphological processes at various temporal
68 scales (Tabacchi et al., 1990; Benda et al., 2004). Riverbank erosion along rivers is one of these natural
69 processes and is necessary to create new pioneer habitat and feed the river's sediment transport flow
70 (Florsheim et al 2008). To limit this erosion in urban areas, riverbanks are often stabilized using bank
71 stabilization structures like dikes, riprap (civil engineering structures made of rocks or concrete) or
72 other civil engineering works.

73 Therefore, riverbeds and riparian habitats are subject to numerous pressures linked to anthropization,
74 in particular through changes in hydrological regime, installation of dams, and channelization of
75 watercourses. Damming and channelization can lead to a loss of habitat and functional connectivity –
76 i.e. the way the landscape structure affects ecological processes like gene flow across landscapes

77 (Wainwright et al., 2011; Baguette et al., 2013). This has been observed in many species such as aquatic
78 macroinvertebrates and fish (Smith et al 2009; Van Looy et al., 2014), but also in riparian plants (Merritt
79 & Wohl, 2006) and mammals, such as otters (Leoncini et al., 2023), whose dispersal is impeded by
80 dams. River embankments with civil engineering structures are usually linked to a loss and/or
81 degradation of natural riparian habitats as they consist in replacing native woody and herbaceous
82 riparian plants to bare ground or rock (Ward & Stanford, 1995; Van Looy et al., 2003; Dudgeon et al.,
83 2006). They also lead to a loss of lateral connectivity by inducing differences between upstream and
84 downstream plant communities (Van Looy et al., 2003; Martin et al., 2021). Loss of connectivity is one
85 of the main causes of biodiversity loss (Haddad et al., 2015; Thomson et al., 2017; Pardini, 2018).

86 Soil water bioengineering (SWBE) bank protection structures are an alternative to ‘hard’ civil
87 engineering structures such as riprap. SWBE structures make it possible to maintain habitats with
88 higher quality and functional diversity (Cavaillé et al., 2015; Janssen et al., 2019), and suitable for more
89 terrestrial and aquatic species (Cavaillé et al., 2013, 2018). For instance, fascine toes (small-diameter
90 willow bundles tied together to form a solid structure) show a higher vegetation cover, a higher
91 abundance of plants, a higher species richness and a lower abundance of invasive alien species than
92 riprap (Cavaillé et al., 2013; Martin et al., 2021). Soil water bioengineering structures can help protect
93 riverbank, while restoring habitats (Rey et al., 2019) and improving habitat connectivity (Martin et al
94 2021). In general, restoring riparian habitats can greatly improve landscape connectivity (Rojas et al.,
95 2020). River managers may therefore wish to restore riparian habitats by replacing civil engineering
96 structures with SWBE structures. However, in highly urbanized areas, hosting a large number of civil
97 engineering bank protection structures, it is unrealistic to replace all of them simply because of
98 financial and technical constraints.

99 Therefore, efforts to identify where restoration would improve habitat connectivity the most can
100 facilitate implementation of SWBE structure. To maximize the positive impact of new restoration
101 projects on landscape connectivity, we need to identify key areas for the dispersal of organisms.

102 Restoration ecology and landscape ecology have provided a wealth of literature on how to prioritize
103 areas for restoration to maximize landscape connectivity (e.g. Hodgson et al., 2011; Tarabon et al.,
104 2019; Bergès et al. 2020). These studies focus in particular on habitat patch creation (Hodgson et al.,
105 2011; Clauzel et al., 2015) or the detection of barriers to movement to remove in priority (McRae et
106 al., 2012; Roy & Le Pichon 2017; Kraft et al., 2019). How to optimize the location of the terrestrial
107 habitats to be restored has been extensively addressed in the literature, but not specifically for riparian
108 habitats. The applied techniques range from least-cost distance calculations based on estimated
109 resistance surfaces (McRae et al., 2012 ; Roy & Le Pichon 2017) to more complex spatially explicit
110 models, e.g. ecological network modeling based on landscape graphs (Clauzel et al., 2015; Avon &
111 Bergès, 2016; Kraft et al., 2019; Clauzel & Godet, 2020). Landscape graphs are models derived from
112 graph theory, a mathematical discipline dedicated to the study of networks. Graph theory applied to
113 landscape ecology borrows some of its concepts from the theory of island metapopulation models. In
114 this conceptual framework, target organisms frequent patches of adapted habitats located in a matrix
115 of non-adapted habitats (Urban et al. 2001). The ease with which organisms can move through the
116 matrix from one habitat patch to another depends on their movement capabilities and the
117 characteristics of the elements composing the matrix. Resistance surfaces are used to model such
118 movements of animals between habitat patches across heterogeneous landscapes. Resistance
119 surfaces are raster layers in which all the elements of the landscape are assigned values indicating their
120 propensity to movement of target organisms. Even if resistance surfaces are largely used for
121 connectivity analyses (Zeller et al., 2012), there is no consensus on how to parameterize them.
122 Resistance values can ideally be derived from empirical data collected in the study area, such as genetic
123 data (landscape genetics), movement data (telemetry), species habitat model (Dufлот et al., 2018;
124 Lalechère & Bergès, 2021) or from a combination of data from the literature and expert opinion (Dutta
125 et al., 2022). The use of landscape graphs and resistance surfaces in landscape ecology makes it
126 possible to calculate specific metrics for quantifying the connectivity of habitats in a spatial network.
127 In particular, the concept of amount of reachable habitat (ARH) focuses on habitat accessibility,

128 including the surface and quality of the habitat patches themselves and their degree of habitat
129 connectivity (Saura et al., 2011). This ARH can be assessed in the form of a single metric (Saura and
130 Rubio, 2010).

131 Connectivity has to be assessed taxon by taxon as species differ in their response to habitat availability
132 and configuration (Vos et al., 2001) and it is rarely possible to carry out detailed analyses for every
133 species. How to select target species to best quantify multi-species landscape connectivity is still under
134 debate in the literature (e.g. Albert et al., 2017; Meurant et al., 2018; Dutta et al., 2023). Meurant et
135 al. (2018) showed that a small number of surrogate species covering different biological traits related
136 to dispersal might adequately represent the needs of the full list of species found in a given habitat
137 type, and provide more informative results than simply maximizing taxonomic diversity of surrogate
138 species. Working with surrogate species is a good way to reconcile conservation objectives with
139 stakeholder constraints and field data availability (Opdam et al., 2008; Wiens et al., 2008).

140 In this study, we proposed a method for prioritizing sections of the riparian habitat for restoration to
141 maximize gains in habitat connectivity restoration to a peri-urban river located in the South East of
142 France. First, based on a multivariate analysis of species traits, we selected several surrogate species,
143 which allowed us to characterize the ability of species to reach available habitats within the riparian
144 ecosystem. For each surrogate species, we used landscape graphs to quantify the importance of
145 riparian habitats to total connectivity. Then, we assessed the contribution of existing and potential
146 SWBE structures, using scenarios. Scenarios were chosen to assess the maximum potential gain in
147 connectivity by replacing all riprap with SWBE structures, or to assess the contribution of existing bank
148 protection structures to connectivity. Finally, in order to prioritize restoration areas, we systematically
149 tested the ability of each potentially restorable bank section along the river to improve habitat
150 connectivity for our surrogate species.

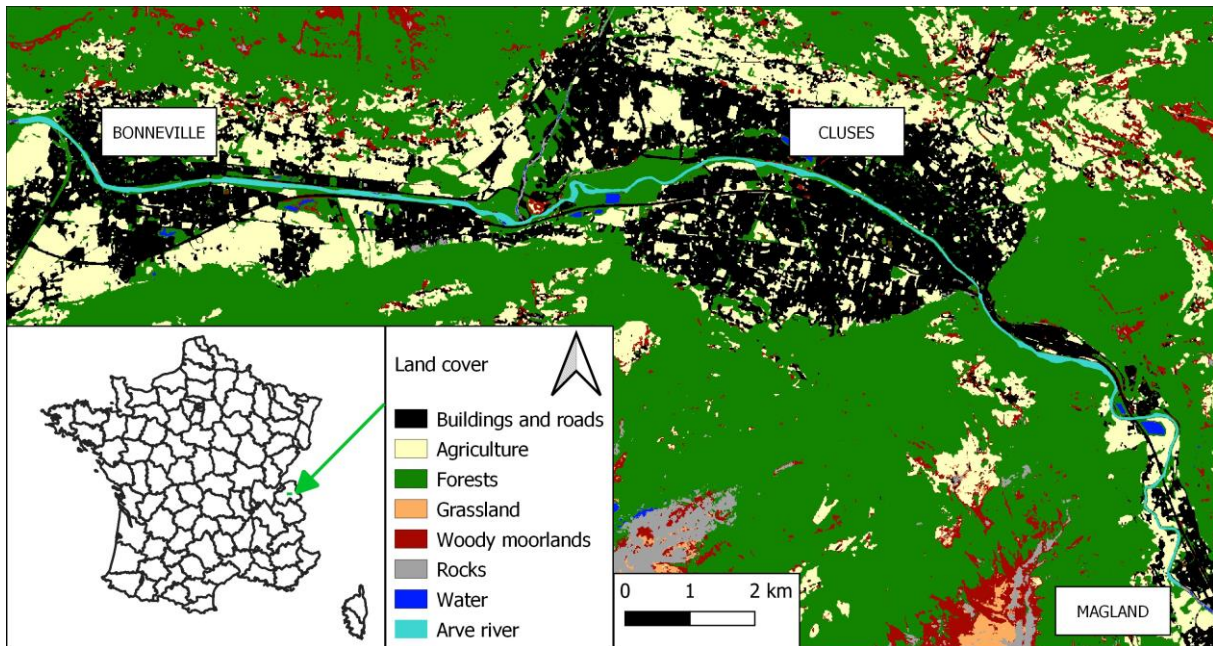
151 We hypothesize that, as each species has different needs and dispersal capacities, the sections that
152 maximize habitat connectivity will differ from one taxon to another. However, the aim of the study is

153 to identify optimal sections that will enable a trade-off to be found to increase habitat connectivity for
154 as many species as possible.

155 **Materials and methods**

156 *Study area*

157 The study area is located in the Haute-Savoie department, France. The section of interest is a 25 km
158 long stretch of the Arve river between the towns of Magland (upstream) and Bonneville (downstream).
159 As the spatial analysis methods used require the use of raster layers, the study area considered is a
160 157 km² rectangle encompassing the 25 km stretch of river studied (Fig. 1). The Arve has a mean annual
161 discharge of 27.4 m³/s (measured at the hydrological station of Sallanches). The elevation in the study
162 site ranges between 440m (Bonneville) and 500m (Magland). It is mainly (54% of the linear) located in
163 an urbanized area (Fig. 1). It is characterized by number of bank protections along the river corridor
164 to control erosion. These protections consist of riprap (46.1% of the total length, see sample photo in
165 the supplementary material), mixed technique (riprap toe with vegetation on the upper part of the
166 bank, 2.2%) or soil water bioengineering structures (live toe willow fascines, 0.5%, see sample photo
167 in the supplementary material). Natural banks represent 51.2% of the total length. The detailed
168 cartography and typology of the bank protections were provided by the river manager (Syndicat mixte
169 d'aménagement de l'Arve et de ses affluents hereafter named SM3A) and supplemented by a field
170 observation campaign along the entire length to verify the information and assess the vegetation
171 height.



172

173 Fig. 1 Land cover map of the study area. Data from France OSO soil mapping (Inglada et al., 2017). The
 174 names of the main towns along the river are shown in white boxes.

175

176 *Selection of surrogate species*

177 Species differ in their response to landscape configuration, i.e. the size and position of habitat patches
 178 and the composition of the landscape matrix (Vos et al., 2001). In order to avoid performing a
 179 connectivity analysis for all the species surveyed in the area, we developed a method to select a few
 180 surrogate species that cover a diversity of biological traits.

181 First, we listed the 54 vertebrate species present in our study area by compiling georeferenced data
 182 from inventories carried out by the SM3A, the natural heritage information system SINP (INPN, 2023)
 183 as well as the data present in the inventories of the zone of floristic and faunistic ecological interest
 184 (INPN, 2023b). As these three sources were not exhaustive in terms of invertebrate inventories, we
 185 limited our analysis to the vertebrates found in the area. The use of vertebrates as umbrella species in
 186 conservation studies is relevant and very common (Yang et al., 2023). The detailed species list is
 187 provided in the Appendix 1 in the supplementary material. Then, for mammals, reptiles and

188 amphibians, we selected only species using watercourses as habitats according to IUCN (environment
 189 5.1 in IUCN nomenclature, see IUCN (2022) for detailed information). For birds, we only selected
 190 species whose main breeding habitats are moving riverbeds, riparian habitats and torrents, according
 191 to the habitat preference classification of Roché et al. (2016), and removed generalist species. Our final
 192 list encompassed 18 species that depend on riparian habitats: five amphibians, 10 birds, two mammals
 193 and one reptile (Table 1).

194

195 Table 1. The 18 candidate species surveyed in the area after retaining only those strictly associated
 196 with watercourses. The four variables (biological traits) used to perform the factor analysis are
 197 indicated, as is the cluster resulting from the hierarchical clustering. Id = unique identifier used for each
 198 species. The paragon species selected for each cluster are in bold.

Id	Group	Scientific name	Common name	Maximum dispersion distance	Maximum longevity (year)	Fecundity per year	Main dispersal mode	Cluster
1	Reptiles	<i>Natrix helvetica</i> (Lacepède, 1789)	Barred grass snake	100m-1km	20	12	Terrestrial and aquatic	2
2	Birds	<i>Actitis hypoleucos</i> (Linnaeus, 1758)	Common sandpiper	+10km	14.5	4	Aerial	1
3	Birds	<i>Alcedo atthis</i> (Linnaeus, 1758)	Common kingfisher	+10km	21	9	Aerial	1
4	Birds	<i>Ardea cinerea</i> Linnaeus, 1758	Grey heron	+10km	37.5	4	Aerial	1
5	Birds	<i>Ardeola ralloides</i> (Scopoli, 1769)	Squacco heron	+10km	5.8	3	Aerial	1
6	Birds	<i>Cettia cetti</i> (Temminck, 1820)	Cetti's warbler	+10km	7,6	6	Aerial	1
7	Birds	<i>Charadrius dubius</i> Scopoli, 1786	Little ringed plover	+10km	13	7	Aerial	1
8	Birds	<i>Mergus merganser</i> Linnaeus, 1758	Common merganser	+10km	14.8	8	Aerial	1
9	Birds	<i>Motacilla cinerea</i> Tunstall, 1771	Grey wagtail	+10km	8	9	Aerial	1

10	Birds	<i>Nycticorax nycticorax</i> (Linnaeus, 1758)	Night heron	+10km	21.1	4	Aerial	1
11	Birds	<i>Riparia riparia</i> (Linnaeus, 1758)	Sand martin	+10km	10	6	Aerial	1
12	Mammals	<i>Castor fiber</i> Linnaeus, 1758	Eurasian beaver	+10km	35	3	Terrestrial and aquatic	3
13	Mammals	<i>Lutra lutra</i> (Linnaeus, 1758)	Eurasian otter	+10km	22	2	Terrestrial and aquatic	3
14	Amphibians	<i>Alytes obstetricans</i> (Laurenti, 1768)	Common midwife toad	100m-1km	7	45	Terrestrial and aquatic	2
15	Amphibians	<i>Bombina variegata</i> (Linnaeus, 1758)	Yellow-bellied toad	1-10km	29	161	Terrestrial and aquatic	3
16	Amphibians	<i>Bufo bufo</i> (Linnaeus, 1758)	Common toad	1-10km	40	9000	Terrestrial	4
17	Amphibians	<i>Pelophylax ridibundus</i> (Pallas, 1771)	Marsh frog	1-10km	12	12000	Terrestrial	4
18	Amphibians	<i>Rana temporaria</i> Linnaeus, 1758	Common frog	1-10km	27	3556	Terrestrial and aquatic	3

199

200

201 We based our species selection on several biological traits that are representative of species ability to
202 reach distant habitats. As we restricted the analysis to those species dependent on a single habitat
203 type (riparian habitats), we did not include habitat preferences in the factorial analysis. Following
204 Henle et al. (2004), we selected traits linked to vulnerability to habitat change: two functional traits
205 related to dispersal capacity (maximum dispersion distance and dispersal mode) and two life history
206 traits related to population dynamics (maximum longevity and fecundity per year). For each species,
207 we collected information on these traits from the literature, using either existing databases and
208 generalist papers (Sutherland et al., 2000; Grimm et al., 2014; Trochet et al., 2014; Myhrvold et al.,
209 2015; Oliveira et al., 2017) or articles more specific to each taxon (Rouland & Migot, 1990; Smith &
210 Green, 2005; Decout et al., 2010; Meister et al., 2010; Quaglietta et al., 2013). Depending on data
211 precision and accessibility in the literature, we coded the traits either as categorical or as continuous
212 variables. The categorical variables were the maximum dispersion distance (coded into the following

213 categories: 0.1-1 km; 1-10 km; >10 km) and the dispersal mode (categories: aerial; terrestrial;
214 terrestrial and aquatic). The continuous variables were the maximum longevity (in years) and the
215 fecundity per year (in number of offspring) (Table1).

216 To select surrogate species, we performed a k-means clustering on these four variables using the
217 Hierarchical clustering on principal components (HCPC), based on a factor analysis for mixed data
218 (FAMD). To do so, we used the functions FAMD and HCPC of the package FactoMineR (Lê et al., 2008)
219 in R environment (R Core Team, 2022). We kept the number of clusters with the highest relative loss
220 of inertia as recommended by Lê et al. (2008). For each cluster, we selected the species located closest
221 to the barycenter as surrogate (thereafter called paragon species).

222 *Habitat characterization*

223 SM3A provided us with a detailed mapping of the habitats along the rivers in the study area. For more
224 remote areas, we used Occupation des Sols (OSO) soil mapping (Inglada et al., 2017), which provides
225 a 23-class land cover map at 10m resolution produced from satellite data. For the aquatic environment,
226 the location of obstacles to flow (weirs) was provided by the SM3A.

227 We treated the riverbanks separately from the rest of the study area. We mapped them using a 10m
228 buffer zone along the Arve River. We determined three characteristics of the banks: type of protection
229 structure, vegetation height and slope. The type of protection structure (5 categories: riprap, lower-
230 bank ripraps with upper-bank plantings, bare rock, natural bank, live toe fascine) and the vegetation
231 height (3 categories: low vegetation cover <25%, mainly herbaceous or shrubby vegetation, mainly
232 tree cover) were mapped in a field survey (2017). The slope was determined using a 1m-resolution
233 digital elevation model obtained by LIDAR and supplied by SM3A. We used two categories: low slope
234 (<60%) and steep slope (>60%). Crossing these three characteristics allowed us to obtain a
235 classification of the banks in $5 \times 3 \times 2 = 30$ categories. 68.1% of the riverbanks were categorized as steep
236 (vs. 32.9% as shallow). Vegetation cover on the banks was sparse (<25%), herbaceous/shrubby and
237 woody on 4.2%, 14.1% and 81.7% of the linear length, respectively.

238 We carried out the cartographic work using QGIS (QGIS.org, 2023). We combined the collected
 239 information in a land use raster map adopting a resolution of 2m, the finest resolution usable by
 240 Graphab software (Foltête et al., 2012, 2021) in our computer configuration (Intel Core i7, 32GB RAM).

241 *Resistance maps*

242 We first determined the main habitat types for each target species, based on literature and discussions
 243 with experts. All patches of potential habitats were mapped within the study area. Then, we classified
 244 the different elements of the matrix according to their resistance to species movement based on
 245 literature and expert opinion. We used the literature to select prior resistance values, which were then
 246 corrected and validated by local naturalist experts. The resistance values were attributed on a
 247 logarithmic scale according to previous papers that demonstrated the importance of using a
 248 contrasted resistance scale in landscape connectivity models (Verbeylen et al., 2003; Clauzel et al.,
 249 2013; Clauzel & Godet, 2020). Our resistance values thus ranged from 1 (habitat patch) to 10,000
 250 (barrier), with a value of 10 assigned to elements favorable to movement, a value of 100 to elements
 251 neutral to movement and a value of 1000 to elements unfavorable to movement (Table 2 and Table
 252 3). The resistance map obtained covered the entire study area (157km²).

253

254 Table 2. Resistance values assigned to the various landscape elements based on literature and expert
 255 opinion, for the 4 surrogate species.

Land cover class	Very favorable	Favorable	Neutral	Unfavorable	Barrier
Resistance attributed	1	10	100	1 000	10 000
Eurasian beaver	Riparian alder and willow groves, rivers	Other deciduous riparian forests	Coniferous	Shrub and bush vegetation, reedbeds, ruderal areas, meadows, crops	Areas located more than 40m from watercourses, buildings, roads, weirs

Common sandpiper	Lakes, reservoirs, rivers, alluvial banks with pioneer vegetation	Reedbeds, wetlands, weirs	Bushes, artificial meadows	Forests, gardens, roads, artificial areas	Buildings, industrial sites, crops
Barred grass snake	Lakes and reservoirs, minor watercourses	Large rivers (Arve), alluvial beds	Forests, bushes, artificial meadows, agricultural areas	Gardens, roads, conifer plantations	Industrial sites, artificial areas, ripraps with joint
Common toad	Deciduous forests, lakes and reservoirs	Minor watercourses, alluvial deposits, reedbeds	Woodlands, coniferous forests, artificial meadows	Gardens, roads	Industrial sites, artificial areas, crops, weirs, ripraps with joint

256

257 Table 3. Resistance values assigned to different riverbanks based on literature and expert opinion, for

258 the 4 surrogate species, depending on their protection structures, vegetation cover and slope.

Species	Slope	Vegetation	Type of bank protection structure				
			Bare zone (cliff, concrete)	Riprap	Lower-bank ripraps with upper-bank plantings	Live toe fascine	Natural bank
Eurasian beaver	Low slope (<60°)	Absent or very sparse (<25% coverage)	1000	1000	-	-	100
		Herbaceous or shrubby vegetation	-	100	10	1	1
		Tree cover	-	100	-	1	1
	Steep slope (>60°)	Absent or very sparse (<25% coverage)	1000	1000	-	100	100
		Herbaceous or shrubby vegetation	-	100	100	1	1
		Tree cover	1000	100	100	1	1
Common sandpiper	Low slope (<60°)	Absent or very sparse (<25% coverage)	10000	1000	-	1	1
		Herbaceous or shrubby vegetation	-	1000	1000	1	1
		Tree cover	-	1000	1000	100	100
	Steep slope (>60°)	Absent or very sparse (<25% coverage)	1000	1000	-	10	10
		Herbaceous or shrubby vegetation	-	1000	1000	10	10
		Tree cover	1000	1000	1000	100	100
Barred grass snake	Low slope (<60°)	Absent or very sparse (<25% coverage)	1000	10	-	100	100
		Herbaceous or shrubby vegetation	-	1	1	1	1
		Tree cover	-	100	100	100	100
	Steep slope (>60°)	Absent or very sparse (<25% coverage)	10000	100	-	1000	1000
		Herbaceous or shrubby vegetation	-	10	10	100	100
		Tree cover	1000	1000	1000	1000	1000
Common toad	Low slope (<60°)	Absent or very sparse (<25% coverage)	10000	10000	-	1000	1000
		Herbaceous or shrubby vegetation	-	1000	1000	10	10

	Tree cover	-	10	10	1	1
Steep slope (>60°)	Absent or very sparse (<25% coverage)	10000	10000	-	100	100
	Herbaceous or shrubby vegetation	-	100	100	10	10
	Tree cover	1000	1000	1000	10	10

259

260 *Assessment of connectivity using landscape graphs*

261 We constructed landscape graphs for each species/scenario combination using Graphab 2.4 software
 262 (Foltête et al., 2012, 2021). To avoid modeling patches too small to constitute real habitats for
 263 vertebrate species, we kept habitat patches larger than 500m² as nodes for the graphs. Graph links
 264 were constructed between all habitat patches, and we only retained the ones that were shorter than
 265 the maximum dispersion distance of each species based on literature. The link impedance between
 266 patches was calculated in least-cost distances based on the previously constructed resistance map.

267 We assessed the landscape connectivity by computing the Probability of Connectivity (PC) index for
 268 each graph. The PC accounts for the amount of reachable habitat for the target species (Saura &
 269 Pascual-Hortal, 2007). It is defined as the probability that two individuals randomly selected within the
 270 landscape are located in interconnected habitat patches. The PC takes into account 1) the total amount
 271 of habitat available, 2) the spatial configuration of habitat patches, 3) the resistance of the landscape
 272 matrix to species movement and 4) the dispersal capacity of the target species modeled:

273
$$PC = \frac{\sum_{i=1}^n \sum_{j=1}^n a_i a_j p_{ij}^*}{A_L^2}$$

274 with a_i and a_j the respective capacities of habitat patches i and j and A_L the total landscape capacity.
 275 We considered habitat patch capacity to be equal to habitat patch area. p_{ij}^* is the maximum value of
 276 the probability of dispersal p_{ij} calculated on all the possible paths connecting patches i and j . p_{ij} is the
 277 direct probability of dispersal between the two habitat patches i and j and is a negative exponential
 278 function of the distance between them d_{ij} in km. :

279
$$p_{ij} = e^{-kd_{ij}}$$

280 k is a constant expressing the intensity of the decrease in the probability of movement (p) with distance
281 (d). The value of k was fixed such that $p_{ij} = 0.05$ when d_{ij} equals the maximum dispersion distance of
282 the target species

283 *Contribution of each habitat type to landscape connectivity*

284 To focus on the importance of each habitat type in the ecological network, we classified habitats into
285 three categories: riverbanks, other river-related habitats (e.g. gravel banks in the middle of the
286 watercourse) and offstream habitats (e.g. pond banks, wetlands). To test each species' level of
287 dependence on riverbank versus offstream or other river-related habitats, we created new graphs,
288 each time removing all habitat patches in a given category. We replaced the removed habitats with
289 matrix elements to which we assigned a resistance value equal to the average resistance of the study
290 area. For each graph, we calculated the PC and the loss of PC compared with the current situation (in
291 %).

292 We scaled this analysis down to the habitat patch level. We also evaluated the importance of each
293 patch of habitats, using the dPC (for delta PC) index calculated with Graphab. dPC is calculated by
294 removing each patch one by one from the network and calculating the associated percentage of PC
295 change. This quantifies the importance of each habitat patch in the spatial ecological network (Saura
296 & Rubio, 2010). To control for habitat patch area, we also calculated the dPC/area index, which
297 quantifies the connectivity importance of each patch per surface unit, which seems appropriate in a
298 context where riverbanks often represent very small surfaces and neighbor larger habitats (e.g. lakes
299 and reservoirs).

300 *Effect of soil water bioengineering structures on habitat connectivity*

301 To investigate the potential for improvement and further degradation in the studied landscape, we
302 drew up three contrasting scenarios of land use change and compared them with the baseline scenario,
303 reflecting the current landscape configuration: 1) the 'riprap to fascines' scenario, or a best-case
304 scenario, in which all riprap structures would be replaced in the study area with low-slope, live toe

305 fascines and plantings above, considered *a priori* to be the most favorable situation for connectivity;
306 2) the 'fascines to riprap' scenario, in which the existing live toe fascines would be transformed into
307 riprap; and 3) the 'fascines and natural banks to riprap' scenario, or worst-case scenario, in which the
308 live toe fascines and all natural banks would be replaced by riprap. The first scenario was designed to
309 assess the potential for improving habitat connectivity through SWBE structures. The second would
310 quantify the contribution of existing live toe fascines to the observed connectivity. The third was
311 designed to assess the contribution of existing natural banks to connectivity. We computed the PC for
312 each scenario and each target species. The PC of the baseline scenario was used to compare the overall
313 connectivity of the ecological network between target species.

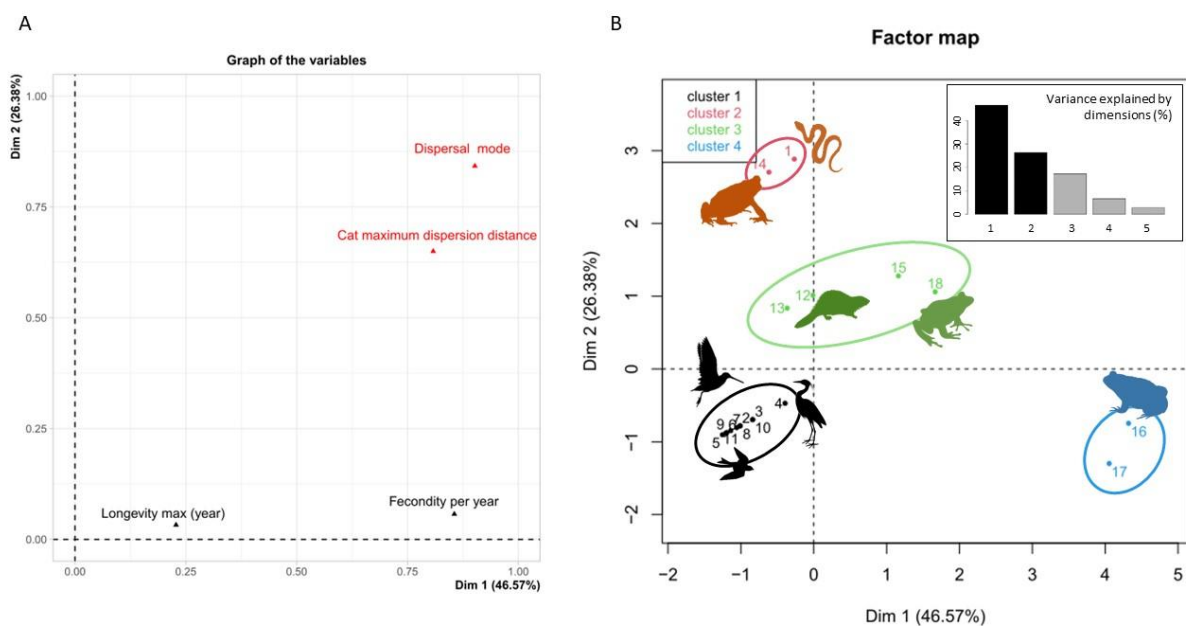
314 *Prioritization of bank sections to restore*

315 As the 'riprap to fascines' scenario is not a realistic short-term development scenario, we tested
316 intermediate scenarios where the manager would only have the means to restore one section of the
317 bank. The aim of this approach was to identify the sections that would offer the highest gain in
318 connectivity for the target species. We first isolated the riprap embankments. Using the QGIS plugin
319 Polygon divider, we divided them into sections of around 100 m in length. For each target species, we
320 then systematically changed the resistance of each section one by one, switching from a riprap
321 resistance value to a live toe fascine resistance value. For each stage (one species and one section), we
322 recalculated the least-cost paths and recreated a graph. For each graph, we calculated PC change,
323 expressed as a percentage of change in connectivity (positive or negative) relative to the baseline
324 scenario. We obtained a change in connectivity for each surrogate species. This made it possible to
325 calculate the impacts of the restoration of any 100 m section, and thus to select those that would
326 maximize connectivity gains once restored. Finally, to test for the sensitivity of this analysis to section
327 size considered, we repeated the operation using 500 m sections (an equally plausible landscape
328 change scenario). A total of 214 sections of 100 m and 77 sections of 500 m were tested one by one.

329 **Results**

330 *Selection of surrogate species*

331 The first two components of the HCPC captured 73% (46.6% and 26.4% respectively) of the variation
332 of the four variables reflecting traits related to dispersal capacity in 18 species (Fig. 2). The variables
333 'maximum longevity' and 'fertility per year' were negatively correlated. At the same time, dispersal
334 mode and maximum dispersion distance appeared to be related (Fig. 2A). In particular, species that fly
335 can disperse over longer distances.



336

337

338 Fig. 2 Factor analysis for mixed data (FAMD) performed on the 18 species and projected into the
339 factorial map formed by the first two components. A: Qualitative and quantitative variables (traits).
340 The continuous variables appear in black while the categorical variables appear in red. B: Species
341 clustered according to their traits. Each point represents a species, and numbers correspond to species
342 identifiers mentioned in Table 2. The hierarchical principal component clustering (HCPC) resulted in
343 four clusters. The silhouettes of some emblematic animals are shown for illustrative purposes

344

345 Hierarchical clustering identified four clusters, each comprising between two and 10 species (Fig. 2B,
346 Table 1). Clusters 1 and 4 were taxonomically homogeneous, being composed of birds and amphibians,
347 respectively. Cluster 2 included one reptile species and one amphibian, while cluster 3 contained two
348 mammals and two amphibians (Table 1). We labeled the clusters according to their main ecological
349 characteristics: “flying animals” (Main dispersal mode = ‘Aerial’), “amphibious weak dispersers” (Main
350 dispersal mode = ‘Terrestrial and aquatic’ and Maximum dispersion distance = “100m–1km’),
351 “amphibious strong dispersers” (Main dispersal mode = ‘Terrestrial and aquatic’ and Maximum
352 dispersion distance = “+10km’) and “walkers” (Main dispersal mode = ‘Terrestrial). The paragon species
353 of these four clusters were the common sandpiper (*Actitis hypoleucos*), the barred grass snake (*Natrix*
354 *helvetica*), the Eurasian beaver (*Castor fiber*) and the common toad (*Bufo bufo*), respectively. These
355 four species were used as target species thereafter.

356 *Contribution of each habitat type to landscape connectivity*

357 For the Eurasian beaver, the main habitats identified (0.29km², 0.2% of the total study area) were
358 wooded banks with no ripraps, with a quiet zone of at least 10m around them, free of any
359 infrastructure (roads, tracks, buildings), as well as water bodies less than 30m from the Arve riverbed.
360 For the common sandpiper, the main habitats (0.29km², 0.2% of the total study area) were gravel
361 banks, riparian vegetation with small cattail and riverbed with herbaceous riparian vegetation. For the
362 barred grass snake, the main habitats (0.52km², 0.3% of the total study area) were lakes and reservoirs
363 banks and low-slope herbaceous stream banks. Finally, for the common toads, main habitats (0.57km²,
364 0.4% of the total study area) were wooded riverbanks with low slopes, lake banks and reservoirs.

365 The highest probability of connectivity (PC) in the study area was found for the common sandpiper (PC
366 = $3.0 \cdot 10^{-6}$), followed by the Eurasian beaver (PC = $2.1 \cdot 10^{-6}$), the common toad (PC = $8.1 \cdot 10^{-7}$) and
367 the barred grass snake (PC = $6.3 \cdot 10^{-7}$).

368 Calculating PC with each habitat type removed one by one, we observed that the Eurasian beaver was
369 the species most dependent on riverbank habitats, which contribute to almost all habitat connectivity

370 for this species (Table 4). The common sandpiper main habitats were gravel banks, which were
 371 classified as 'other river related habitats'. Habitat connectivity for the common toad depended on both
 372 riverbank and offstream habitats. Connectivity for the barred grass snake was mainly linked to
 373 offstream habitats (Table 4). Note that it is normal for the sum of PC losses for each species to be
 374 >100%, as several habitat patches of different types may be redundant in terms of connectivity.

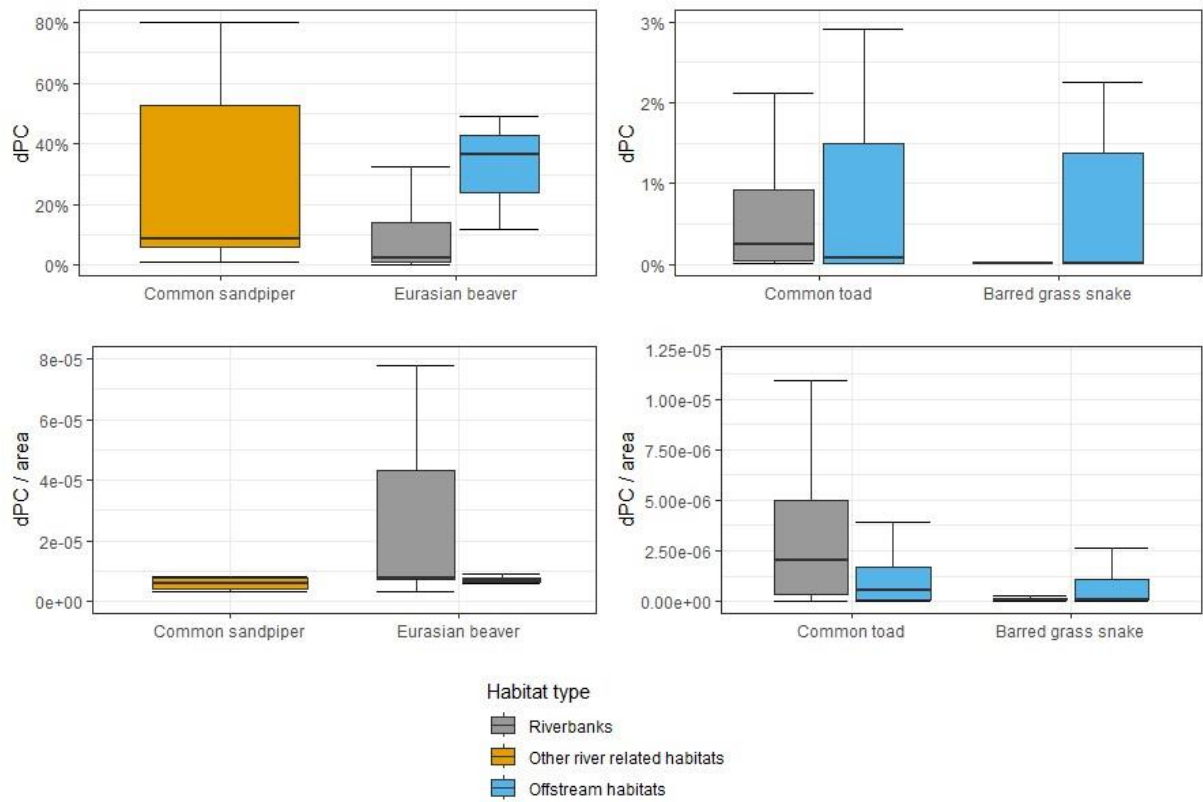
375 Table 4. Variation in PC obtained by removing each habitat type one by one. It is expressed as a
 376 percentage loss compared with the current situation.

Species	Loss of PC if removed		
	Riverbank habitats	Other river related habitats	Offstream habitats
Common sandpiper	-	100%	-
Common toad	60.1%	-	52.4%
Eurasian beaver	99.9%	-	4.8%
Barred grass snake	28.0%	-	75.5%

377

378 Calculating the dPC for each habitat patch showed that for the Eurasian beaver and the barred grass
 379 snake, each offstream habitat patch contributed more in absolute values to total network connectivity
 380 than riverbank habitat patches. To a lesser extent, this was also the case for the common toad. In our
 381 landscape, the only habitats of the common sandpiper were gravel banks (classified as 'other river
 382 related habitats'), so no comparison across habitat types was possible. When controlling the
 383 contribution of habitat patch to overall connectivity by habitat patch area (dPC/area), riverbank
 384 habitats appeared to contribute more to overall network connectivity than offstream habitats for the

385 common toad and the Eurasian beaver. The trend remained the same for the barred grass snake (Fig.
 386 3).



387
 388 Fig. 3 Boxplot of the distribution of the delta Probability of connectivity (dPC) computed for each
 389 habitat patch, differentiating between riverbank habitats, other river-related habitats (mainly gravel
 390 banks) and offstream habitats. Top: dPC is shown as a percentage of PC change. Bottom: dPC is divided
 391 by patch area to eliminate the 'area effect' associated with the PC calculation method. We separated
 392 species into two groups for easier reading

393
 394 *Impact of landscape change scenarios*

395 The live toe fascines were identified as very favorable environments (resistance = 1) for the Eurasian
 396 beaver and common toad, and neutral (resistance = 100) for the common sandpiper and barred grass
 397 snake (Table 3). The 'riprap to fascines' scenario responded in an average increase in PC of 15% for the
 398 four target species. The 'fascines to riprap' scenario had no effect (+0%), while the 'fascines and natural

399 banks to riprap' scenario corresponded to a PC decrease of 2%. However, these values masked strong
 400 differences among species. The barred grass snake (amphibious low disperser) and the common
 401 sandpiper (aerial disperser by flight) were insensitive to any bank modifications. In contrast, the 'riprap
 402 to fascines' scenario increased connectivity by 46% and 14% for the Eurasian beaver (amphibious high
 403 disperser) and the common toad (walker), respectively. For these two species, the 'fascines and natural
 404 banks to riprap' scenario led to a decrease in PC of 4% and 5%, respectively (Table 5).

405

406 Table 5. Percentage change in probability of connectivity (PC) relative to the baseline scenario, for each
 407 species and each scenario.

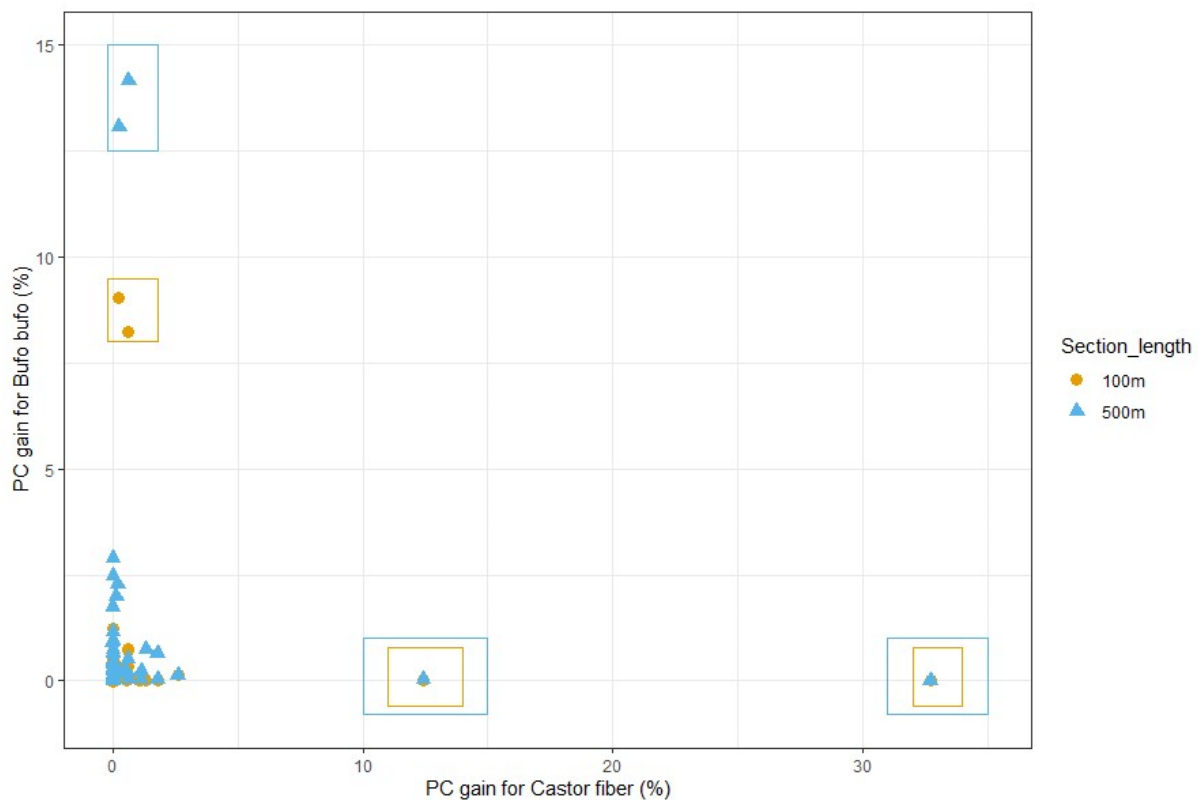
Species	Scenarios		
	Riprap to fascines	Fascines to riprap	Fascines and natural banks to riprap
Common sandpiper	0%	0%	0%
Common toad	+14%	0%	-5%
Eurasian beaver	+46%	0%	-4%
Barred grass snake	0%	0%	0%

408

409 *Prioritization of bank sections to restore*

410 As the analysis of the different scenarios showed that two of the four species (the common sandpiper
 411 and the barred grass snake) were insensitive to bank modifications, the prioritization of the sections
 412 to restore was only made for the other two species (Fig. 4). Whatever the section length (100m or
 413 500m), the vast majority of the sections tested had little or no effect on connectivity if they were the
 414 only ones to be restored. Thus 98.1% (210/214) of the 100m sections and 94.8% of the 500m sections

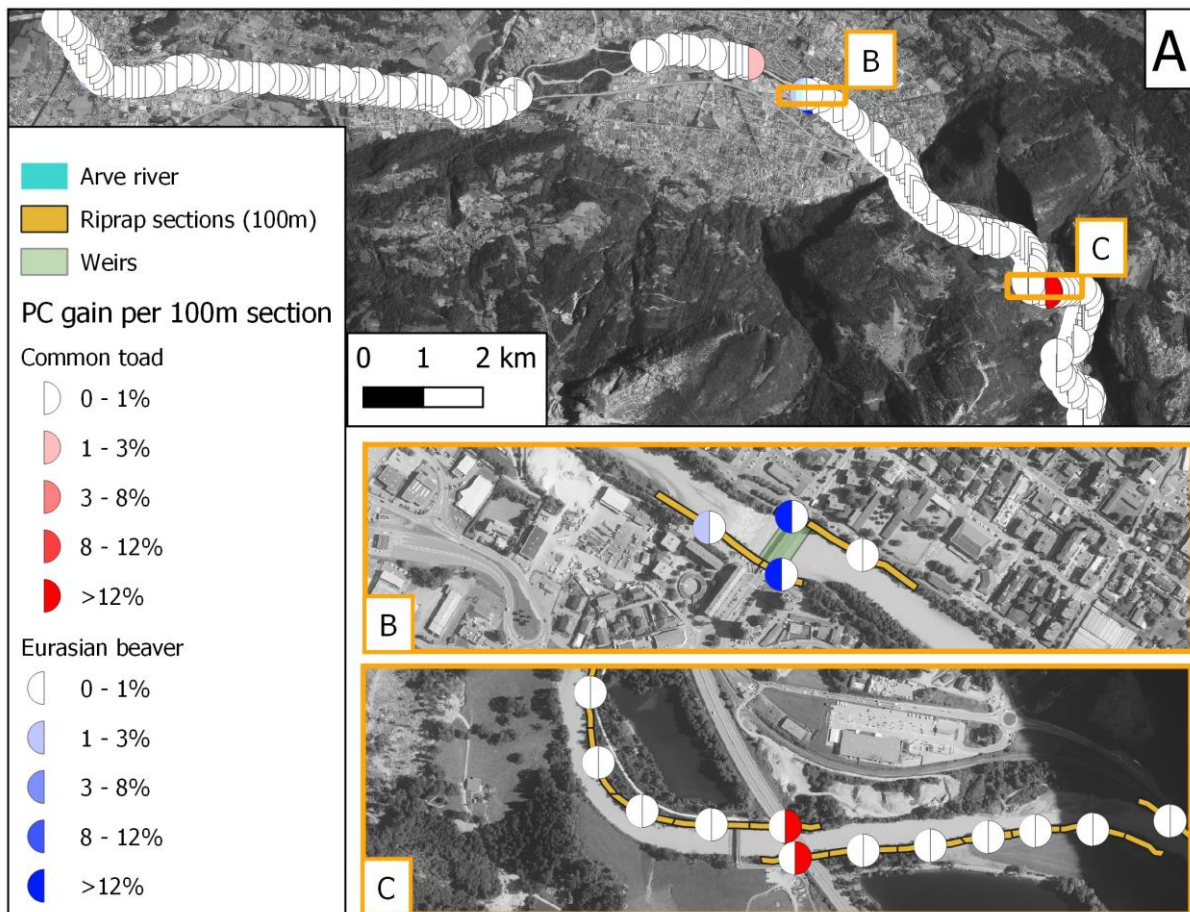
415 (73/77) increase the PC of any species by less than 3%. Only four 100m sections and four 500m sections
 416 offered greater potential for connectivity improvement. Over the 100m sections, two of them would
 417 improve PC for common toad by more than 7.5% and two would improve PC for beaver by more than
 418 12%. For the 500m sections, two significantly improved connectivity (gain above 5%) for common toad
 419 (+13.1% and +14.2% respectively), and two for Eurasian beaver (+12.4% and +32.7% respectively).
 420 However, the sections that best improved connectivity could only do so for a single target species at a
 421 time. In other words, the most favorable sections for the Eurasian beaver did not at all intersect with
 422 the most favorable sections for the common toad.



423
 424 Fig. 4 Gains in habitat connectivity for two target species achieved by replacing riprap sections with
 425 live toe fascines. The orange dots represent 100 m sections, while the blue triangles represent 500 m
 426 sections. The gain in connectivity for each species (Eurasian beaver *Castor fiber* and common toad *Bufo*
 427 *bufo*) is expressed as the PC gain relative to the PC of the baseline scenario. Rectangles highlight
 428 sections with a significant gain in connectivity (above 5%) for a given species

429

430 Fig. 5 confirmed that the sections favorable to the two target species were different and distant. The
431 high-priority sections for the restoration of Eurasian beaver riparian corridors were located in the town
432 of Cluses, on either side of a weir (B). The high-priority sections for the restoration of common toad
433 riparian corridors were located upstream (east) of the study area, under the bridge over which the
434 highway crosses the Arve river (C). The location of the sections to restore did not change when we
435 used 500m sections, which suggests that at this spatial scale the prioritization does not depend on the
436 length of the section considered (see Appendix 3 in the supplementary material).



437

438 Fig. 5 PC gain obtained by replacing one by one 100m riprap section with a live toe fascine. Sections
439 are represented by circles for visibility. As each section is tested for two species, the circles are divided
440 in two. The gain in connectivity is represented by a gradient of blue (Eurasian beaver) or red (common
441 toad). We provided detailed inserts B, C for greater readability

442

443 **Discussion**

444 We showed that using soil water bioengineering (SWBE) structures instead of civil engineering for
445 riverbank protection could greatly change landscape connectivity for some species, while showing no
446 effect for others. Our results showed that not all tested vertebrate species responded in a similar way
447 to changes in riverbank structures, some of them not responding at all (common sandpiper and barred
448 grass snake). Restoring small, well-positioned bank sections could lead to significant gains in
449 connectivity for certain species like the Eurasian beaver or the common toad. However, sections that
450 simultaneously favor all taxa were not detected.

451 *Selection of surrogate species*

452 We used a method for selecting surrogate species based on the use of species traits linked to sensitivity
453 to landscape fragmentation. This method was mainly based on data from generalist databases
454 covering a wide number of species (Grimm et al., 2014; Trochet et al., 2014; Myrvolt et al., 2015) and
455 is therefore easily transposable to other case studies. However, for some species, more specific
456 literature would be required for conducting this analysis. In our study, this was particularly the case
457 for certain reptile and amphibian species, for which the literature is less extensive than for birds and
458 mammals.

459 Our method enabled us to highlight four clusters of species, and therefore four surrogate species, to
460 represent the diversity of traits related to dispersal capacities and life cycle present in our pool of
461 candidate species. This number of species was slightly lower than the results of Meurant et al. (2018),
462 who used an initial list of 296 vertebrate species – compared with 18 in our study, which probably
463 corresponds to a much greater diversity of biological traits. In this configuration, they demonstrated
464 that selecting 5 to 7 species based on traits was generally sufficient to retain the majority of 84
465 conservation criteria. The use of surrogate species representative of their cluster, rather than virtual
466 species in connectivity analysis, seems also better suited to communicate with river managers and

467 decision-makers. Generalist species that use riparian habitats may also be sensitive to bank
468 modifications. Nevertheless, we have chosen to include only specialist species in the analysis, which
469 are particularly sensitive to landscape modifications (Devictor et al., 2008; Keinath et al., 2017). We
470 believe this conservative approach is relevant to environmental management research.

471 Unsurprisingly, the factorial analysis showed that the variables 'maximum longevity' and 'fertility per
472 year' were negatively correlated. This is a good example of the r/K dichotomy (Pianka, 1970), which
473 explains why there's always a trade-off between quality and quantity of offspring. The so-called r
474 species (mainly represented by the amphibians in our study) have a reproductive strategy that enables
475 them to deal with major variations in the availability of vital resources. They are characterized by short
476 life spans and high annual fecundity. K species invest more in the survival of their young in a context
477 of predictable access to resources. They are characterized by a long lifespan and low annual fecundity.
478 On the other hand, there were a statistical relationship between dispersal mode and maximum
479 dispersal distance. In particular, species capable of flight are able to disperse further, while the walking
480 group disperses over shorter distances. The four clusters identified, "flying animals", "amphibious
481 weak dispersers", "amphibious strong dispersers" and "walkers", appeared to be ecologically coherent.
482 The fact that they were not all taxonomically homogeneous is consistent with the results of Meurant
483 et al. (2018) who showed that grouping the species by taxon was not necessarily the most appropriate
484 approach.

485 *Connectivity analysis and riverbank change scenarios*

486 PC ranking mainly reflected the target species's dispersal capacities in the studied landscape. It was
487 logical to find that connectivity of the landscape was highest for the common sandpiper first, as birds
488 are naturally less sensitive to landscape fragmentation and barriers compared to other taxa such as
489 reptiles (Keinath et al., 2017). Next came the Eurasian beaver, which disperses mainly along
490 watercourses (Table 2) followed by the common toad and barred grass snake, which disperse mainly

491 along terrestrial habitats and are therefore more sensitive to the quality of the landscape matrix
492 (Keinath et al., 2017).

493 Interestingly, scenario analysis revealed significant disparities between species (Table 5). The common
494 sandpiper was not sensitive to changes in riverbank structures, which can be explained by its ability to
495 fly and high dispersal distances. Changing from riprap to vegetated banks and vice versa had little
496 impact on it, particularly as its main habitat is gravel banks in the middle of watercourses. The
497 importance of gravel banks in landscape connectivity for this species was therefore significant (Fig. 3).

498 The barred grass snake (*Natrix helvetica*) had some dependence on riverbanks (Table 4). However, it
499 did not appear to be sensitive to riverbank change scenarios at all (Table 5). This can be explained by
500 the fact that riprap banks and fascines were categorized neither as favorable habitats, nor as elements
501 that particularly impede this species movements. Experts therefore assigned them an equal resistance
502 value (100) (Table 3). Consequently, switching from one type of bank to another as part of the scenario
503 did not affect landscape connectivity for this species. This result is interesting from a management
504 perspective, as it shows that ecological restoration is not necessarily favorable for all species,
505 particularly species that are well adapted to human infrastructures or degraded habitat (Walts &
506 Wallace Covington, 2004; Noreika et al., 2015).

507 The analysis of connectivity for Eurasian beaver (*Castor fiber*) and common toad (*Bufo bufo*) showed
508 that both species seemed to be highly dependent on riverbank habitats for their connectivity (Table
509 4). The 'riprap to fascines' scenario greatly improved connectivity, while the 'fascines and natural banks
510 to riprap' scenario reduced it (Table 5). The 'fascines to riprap' scenario only concerned the
511 replacement of the single live toe fascine in the landscape (0.5% of the total bank linear), so its impact
512 on connectivity was expected to be low. The dPC analysis showed that offstream habitats could be
513 very important for habitat connectivity in absolute value (Fig. 4). This was particularly the case for the
514 Eurasian beaver, which occurs in offstream water bodies that can cover large areas of the study zone
515 (Table 2). When divided by surface area (dPC/area), the importance of riverbank habitats for ecological

516 connectivity appeared to be greater, highlighting their disproportionate ecological importance in
517 relation to their surface. Their importance had already been demonstrated by Sabo et al. (2005), who
518 showed that riparian habitats increased regional species richness by >50% on average worldwide,
519 despite their narrow surface area. Riparian habitats are therefore what Hunter (2017) calls small
520 natural features with large ecological roles. Nevertheless, maintaining favorable offstream habitats in
521 addition to riverbank habitats for semi-aquatic species seems to be a good solution for maintaining or
522 improving landscape connectivity. This is particularly the case for species that are not strictly river-
523 dwelling, such as the common toad and the barred grass snake (Table 3). This result is consistent with
524 previous studies showing the importance of the offstream wetland network in ecological connectivity,
525 particularly when riverbed habitats are subject to change as a result of hydromorphological variations
526 like flooding (Karim et al., 2012). Our study shows that this is also the case in urbanized areas, which
527 are much less subject to hydromorphological variations due to the channelization of rivers. This study
528 is based on resistance surfaces parameterized based on expert opinions and the literature. It could be
529 useful to supplement it with field studies on the actual movements of species, for example using
530 genetics or telemetry.

531 *Prioritization of bank sections to restore*

532 Our prioritization analysis showed that at the tested scale (100 and 500m-long sections) there was no
533 single section where restoration would maximize connectivity for all the target species. On the
534 contrary, the majority of sections tested had only a limited effect on connectivity when considered
535 separately (PC gain < 3%). The few sections with a strong effect were only effective for one species at
536 a time, either the Eurasian beaver or the common toad (Fig. 4). Multi-species connectivity studies often
537 reveal inter-taxon disparities in response to habitat change (e.g. Albert et al., 2017; Meurant et al.,
538 2018). It is noteworthy that a few sections have a very high potential for increasing connectivity, and
539 their restoration alone would allow to achieve or approach the level of connectivity of the best case
540 ('riprap to fascines') scenario. For example, one 500m section would increase connectivity for common

541 toad by 14%, which is the potential total gain of the 'riprap to fascines' scenario in the studied riverine
542 landscape. For Eurasian beavers, a single section can increase PC by more than 32%, close to the total
543 gain of 46% for the 'riprap to fascines' scenario.

544 A cartographic analysis of the location of the sections tested showed that there were key sectors of
545 the river where the priority sections to restore were concentrated. These were areas whose position
546 in the habitat network made the reduction of their resistance to movement particularly interesting for
547 connectivity. For example, panel B (Fig. 5) showed that the most interesting sectors to restore in terms
548 of habitat connectivity for Eurasian beavers were located on either side of a weir in an urban
549 environment. The weirs were identified as potential barriers to beaver longitudinal movement (Table
550 2). As the concerned weirs were located in urban areas, the environments above the banks were not
551 crossable by beavers (built-up areas). The fact that the beavers could cross the banks laterally (10m
552 wide) were not sufficient to enable them to reach areas favorable to movement. They therefore
553 needed to travel a longer distance along the banks to bypass the weirs and move from one section of
554 the river to another. This cost of movement would be reduced by replacing riprap with SWBE
555 structures, improving the crossability of the banks to improve habitat connectivity. Panel C (Fig. 5)
556 contained the main sectors to restore for the common toad. These were located under the highway
557 bridge. As the highway itself is a strong barrier to toad movement, being able to pass underneath it
558 would increase habitat connectivity between downstream and upstream. This could be made possible
559 by replacing the bank riprap under the freeway bridge with a fascine, which is more permeable to toad
560 movement than riprap.

561 Our analysis therefore showed that the restoration of small, well-chosen areas of riverbanks could
562 enable semi-aquatic animals to avoid ecological barriers present in urbanized landscapes (buildings,
563 roads) or in riverbeds (weirs). Detecting and removing barriers to movement to improve connectivity
564 is a well-known issue in landscape ecology, in both terrestrial (McRae et al., 2012) and aquatic contexts

565 (Kraft et al., 2019). In the case of the Eurasian beaver, it is likely that the same result could be achieved
566 by removing the barrier in the riverbed (weir) as by restoring the surrounding banks.

567 The prioritization analysis was not very sensitive to the size of the sections tested. We could expect
568 that switching from 100m to 500m sections should reveal new favorable zones, but the most favorable
569 zones to restore did not change (Appendix 3). The switch just revealed low-priority areas (potential PC
570 gain <3%) for the common toad and the Eurasian beaver. However, high-priority areas were
571 immediately apparent when testing 100m sections. The switch to 500m only confirmed the potential
572 PC gain (Fig. 4, Appendix 3).

573 *Conclusion: insight for management*

574 Our study proposes a valuable decision-making method to help river managers determine where to
575 restore bank protection structures using soil water bioengineering. As many species with variable
576 dispersal capacities may be present in the study area, we recommend that managers rely on accurate,
577 up-to-date species inventories to guide management choices. We showed that it can be difficult to
578 satisfy the needs of all riparian habitat species when selecting a section to restore. This result supports
579 previous studies showing that different riparian species can respond differently to deleterious changes
580 in their environment (e.g. Van Looy et al., 2013). It seems logical to obtain similar results for a priori
581 more favorable changes in the landscape, such as ecological restoration. To improve habitat
582 connectivity in a multi-species context, it may be worthwhile to restore several small, appropriately
583 located sections according to the ecological requirements of several target species. It may also be
584 worthwhile to focus on one or two species of particular concern (e.g., a species with high conservation
585 value) to limit the number of target species with different ecological needs. As the restoration of
586 connectivity is not necessarily at the heart of all restoration projects, this choice of target species can
587 be made as part of a more general framework for defining the objectives of the restoration project
588 (Hallett et al., 2013; Coutinho et al., 2023). We believe that our method will find its place as a decision-
589 making tool for planning restoration projects, alongside others from other fields that may include other

590 areas of ecology as well as governance or economic benefit criteria that may be crucial to the chances
591 of success of ecological restoration projects (Hallett et al., 2013).

592 **Authors' contribution**

593 AE, LB and MA designed the study. BD and TH performed the field work. EB performed the analysis
594 and led the writing of the manuscript. AE, LB, MA and EB contributed critically to the drafts and gave
595 final approval for publication.

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