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1 **Does soil bioengineering benefits instream biodiversity? An empirical study of the relative**
2 **influence of local and regional drivers on benthic macroinvertebrate assemblages**

3

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11 **Abstract**

12 Riverine ecosystems form a dendritic network in which landscape and catchment-scale properties
13 influence freshwater community structure. Placed in a restoration framework, this suggests that
14 regional drivers can overrule the benefit of measures aiming at improving local habitat quality.
15 Disentangling the relative influence of local and regional drivers on freshwater communities is thus
16 crucial for ecosystem management and restoration. Along riverbanks, soil bioengineering is often
17 used to both control erosion and improve ecological conditions. Soil bioengineering techniques aim
18 at copying naturally functioning riverbank models and can thus be viewed as riparian ecosystem
19 restoration. Nevertheless, these techniques are mostly designed at the local scale and are
20 implemented in a broad range of rivers. This implies large variations in regional drivers, which may
21 greatly influence the response of freshwater communities to restoration efforts. We studied 37
22 riverbanks, from civil engineering to soil bioengineering, plus natural willow stands, in the foothills of
23 the Alps and Jura Mountains, and assessed the relative influence of local (terrestrial and aquatic
24 habitat conditions) and regional (water quality, hydrological context and land cover composition)
25 drivers on benthic macroinvertebrate assemblages. Using multivariate GLM and structural equation
26 modelling, we investigated variations in the taxonomic and functional composition and in the
27 diversity of native, exotic, shredder and scraper taxa to both set of drivers. Our results show that soil
28 bioengineering improved local habitat conditions, with an increase in the vegetation density and in
29 the aquatic habitat quality. Related changes influenced the functional composition but not diversity
30 patterns. Instead, we found that natives and shredders richness increased from civil engineered to
31 soil bioengineered structures. This direct influence of riverbank protection techniques suggest that
32 soil bioengineered improves instream habitat quality by inducing other changes in local abiotic
33 conditions (i.e., shade, water temperature, input of organic material). However, our results also show
34 that macroinvertebrates were more influenced by regional than by local drivers. Thus, the
35 hydrological context best explained the composition of taxa feeding habits and variation in taxa
36 diversity, with larger abundance and richness of scrapers and shredders in small headwater streams.

37 Land cover ranked second in explaining variations in functional composition. Also, the diversity of
38 natives, scrapers and shredders increased with a decreased proportion of urban dominated
39 landscapes. Finally, the abundance of scrapers and natives increased with water quality, while the
40 richness of exotic species decreased. Overall, these results highlight the hierarchical structure of local
41 and regional drivers on freshwater communities. Along river networks, catchment-scale properties
42 and landscape attributes are major drivers of macroinvertebrate assemblages. Soil bioengineering
43 improves habitat quality and as such appears to be a good compromise solution to control erosion
44 and support freshwater communities, even though this nature-based solution cannot solve
45 anthropogenic pressures at larger scales. To improve the efficiency of restoration efforts, integrated
46 approaches accounting for both local and regional drivers remains a priority.

47

48 Keywords: benthic macroinvertebrates, community structure, ecological restoration, exotic species,
49 soil bioengineering

50 **1. Introduction**

51 Advances in ecological theory, formalized within the metacommunity concept (Leibold et al., 2004),
52 have evidenced that community assembly resulted from the joint action of local – i.e niche-based –
53 and regional – i.e., dispersal – drivers. The ability of organisms to disperse and colonize areas is
54 largely dependent on landscape attributes, i.e., variations in habitat area, quality and connectivity
55 and properties of the matrix environment (Hodgson et al., 2011). Thus, beyond the availability of
56 local suitable habitat conditions, community composition in targeted areas remain largely dependent
57 on landscape attributes at multiple scales (e.g., Bruno et al., 2014; Kail and Wolter, 2013; Stoll et al.,
58 2016; Townsend et al., 2003). In a context of ongoing global biodiversity loss (Butchart et al., 2010)
59 and in order to enhance our understanding of biodiversity patterns, it therefore appears of primary
60 importance to balance the relative influence of local and regional drivers.

61 Lotic ecosystems are intrinsically structured in a hierarchical way (Ward, 1989) and form a dendritic
62 network in which landscape structure and physical flows dictate dispersal events (Altermatt, 2013).
63 Changes in community structure cannot thus be explained by considering a single set of local habitat
64 variables, but a combination of local and regional drivers (Kuglerová et al., 2015). Investigating the
65 impact of multiple stressors on freshwater communities, Leps *et al.* (2015) showed that linkages
66 between communities and different scales of land use and stream type groups varied strongly,
67 suggesting that the improvement of local habitat conditions might be overwhelmed by catchment
68 and landscape-scale properties. Placed in a restoration framework, this suggests that the benefit of
69 measures aiming at improving local habitat quality can be overruled by regional drivers (Palmer et
70 al., 2010). Indeed, a few studies have documented how the success of river restoration on benthic
71 macroinvertebrate communities depends on the species pool in surrounding areas (Sundermann et
72 al., 2011; Tonkin et al., 2014), the regional hydromorphological habitat quality (Stoll et al., 2016) and
73 the position of the restored reach within the river network (Swan and Brown, 2017). To achieve long
74 lasting successes in ecological restoration, it is thus of vital importance to consider the influence of
75 potential large-scale drivers.

76 In riparian zones, nature-based solutions are often used to both control erosion and improve
77 ecological conditions along riverbanks (Keesstra et al., 2018). By using the physical properties of
78 living plants, soil bioengineering techniques aim at copying naturally functioning riverbank models
79 and can thus be viewed as riparian ecosystem restoration (Rey et al., 2019). Indeed, through the
80 active introduction of pioneer native tree and shrub species, soil bioengineering have been showed
81 to increase riparian habitat quality and biodiversity (Janssen et al., 2019; Li et al., 2006; Schmitt et al.,
82 2018), as compared to civil engineering solutions. The ecological benefit of soil bioengineering are
83 however not only restricted to the terrestrial part of the riverbank. By increasing tree coverage and
84 diversity, these stabilization structures may induce changes in river abiotic conditions (i.e., light,
85 temperature, flow velocity, sediment deposition, water quality) and foster greater input of organic
86 material in riverbed (Corenblit et al., 2007; Cummins et al., 1989; Garner et al., 2017; Osborne and
87 Kovacic, 1993), which directly benefit aquatic biodiversity (Cavaillé et al., 2018; Pander et al., 2017;
88 Sudduth and Meyer, 2006). Nevertheless, soil bioengineering techniques are mostly designed at the
89 local scale and are implemented in a broad range of rivers, from mountain streams to large alluvial
90 rivers. This imply large variations in the properties of regional attributes (e.g., water quality,
91 hydrological conditions and landscape composition), which may greatly influence the structure of
92 freshwater communities and their response to restoration efforts.

93 Here, we aimed to study how different riverbank structures, including civil engineering, soil
94 bioengineering and natural willow stands, influence the diversity and composition of benthic
95 macroinvertebrates in the French and Swiss foothills of the Alps and Jura Mountains. Beyond the
96 direct effect of the type of structure (Cavaillé et al., 2018), we wanted to assess the relative
97 ecological added-value of soil bioengineering techniques on benthic macroinvertebrate communities
98 as compared to influential regional drivers. Indeed, though our study design was built in a way that
99 limits significant variations in confounding factors between treatments, we could not avoid quite
100 large variations in hydrological, land-cover and water quality conditions within treatments. Thus,
101 moving beyond simple categories of riverbanks, we took advantage of these variations to contrast

102 the influence of local and regional drivers on benthic macroinvertebrates. By using a taxonomic and a
103 functional approach, we aimed to understand whether the ecological benefit of using soil
104 bioengineering techniques to stabilize riverbanks can be overruled by catchment and landscape-scale
105 properties. From a restoration perspective, this was done to identify which are the key factors in
106 stabilization structure, and regional environmental conditions, that has the best potential for hosting
107 diverse benthic macroinvertebrate communities, and thus increase the effectiveness of stream
108 restorations (Bernhardt and Palmer, 2011).

109

110 **2. Materials and Methods**

111 **2.1. Study area and sampling design**

112 The study was carried out in the French and Swiss foothills of the Alps and Jura Mountains (Fig. 1),
113 which are characterized by a limestone substratum and a temperate climate. We selected a large
114 array of rivers (n = 23), between the Drôme River (44°43'N; 4°58'E) and the Doubs River (47°21'N;
115 7°10'E), at elevations ranging from 200 to 700 m asl. The area of the upstream watersheds of the
116 sampled rivers ranged from 5 to 5,700 km² and was occupied to a large extent by forested areas (48
117 %) and agricultural areas (39 %) and to a lesser extent by sparsely vegetated areas (8 %) and urban
118 areas (5 %).

119 In 2011, we sampled 37 riverbank sites: 29 were engineered for erosion control and 8 were young
120 natural riparian willow stands (Table A.1., see also Cavaillé et al., 2018). Among the engineered
121 riverbank sites, four different stabilization structures were investigated: riprap protection (n = 8),
122 mixed protection, i.e., riprap at lower part combined with soil bioengineering at the upper part of the
123 bank (n = 7), vegetated crib wall (n= 6) and willow fascines (n= 8). All streambank protection occurred
124 between 3 and 9 years prior to the study.

125 **2.2. Benthic macroinvertebrates assessment**

126 Benthic macroinvertebrates were sampled following a standardized protocol (AFNOR, 2009), in
127 September and October 2011. To explore a representative range of aquatic habitats along each

128 riverbank site, five surber samples (500 μm mesh size, sampling area of $1/20 \text{ m}^2$) were taken in the
129 five most qualitative submerged habitats (see 2.3. for details). Incremental samples were taken from
130 downstream to upstream to avoid any disturbance caused by walking in the riverbed. The material
131 collected was fixed in 70 % ethanol and sorted in laboratory. Independent experts identified benthic
132 macroinvertebrates to the lowest practical taxonomic level.

133 To avoid identification or quantification bias in the analyses, the taxa Hydrozoa, Bryozoa, Porifera,
134 Hydrachnidia, Nematoda and Oligochaeta were removed from the dataset and taxon identifications
135 were harmonized at the family level (Floury et al., 2013). In addition, to highlight how soil
136 bioengineering techniques, as well as regional drivers, induce changes in diversity patterns, we
137 distinguished between native and exotic species in subsequent analyses (i.e., based on species
138 chorology and expert knowledge, Table A.2.). Focus was made on exotic species because they
139 represent potential threats to native communities and pose challenges to restoration measures
140 (Leuven et al., 2009; Strayer, 2010). Finally, beyond the taxonomic approach, we used a functional
141 approach by considering groups of species based on their feeding habits. Specifically, we considered
142 the affinity of each taxa to 8 categories describing behavioural aspects of nutrition: absorber,
143 deposit-feeder, shredder, scraper, filter-feeder, piercer, predator and parasite (Tachet et al., 2010).

144 The affinity index is an integer score ranging from 0 (no affinity) to 3 (strong affinity), based on expert
145 knowledge, which integrates possible variation in feeding habits during the life stage of a taxa.

146 Following Bady et al. (2005), this index was treated as frequency distribution which allowed us to
147 compute a new matrix giving approximate abundances for each class of feeding habits at each
148 riverbank site (see raw data in Table A.2.). We then decided to more specifically focus on diversity
149 patterns of shredders and scrapers, because these feeding groups rely on coarse organic material
150 and are dominant in headwaters (Vannote et al., 1980). Indeed, given that input of organic material
151 are expected to be higher along riverbanks stabilized by soil bioengineering, as compared to those
152 stabilized by civil engineering, shredders and scrapers were hypothesized to be the best candidates
153 to investigate the relative influence of local and regional drivers on macroinvertebrates.

154 **2.3. Riparian habitat variables**

155 To assess the effect of soil bioengineering on benthic macroinvertebrates, we used three terrestrial
156 and three aquatic habitat variables that were expected to highlight differences in habitat quality
157 among riverbank structures (Table 1). For the terrestrial part of bank, we considered the cover density
158 of herbaceous, ligneous and exotic plant species. Data were extracted from riparian vegetation
159 surveys, conducted from May to July 2011, along three 25 m transects located parallel to the
160 riverbank (i.e., one transect close to the water line, one in the middle and one on the upper part,
161 close to the edge of the riverbank). Along each transect, measurements of plant species frequency
162 were taken every meter using the Point Contact Method. For the aquatic part of the bank, we
163 considered the richness of habitats and the percentage cover of low and high potential habitats for
164 macroinvertebrates. Data were extracted from substrate inventories, conducted from September to
165 October 2011 along each submerged part of riverbank. Substrates covering more than 1/20 m² were
166 assessed and assigned to one of the 12 following substrate types: slab (Hab = 0), algae (Hab = 1),
167 sand/silt (Hab = 2), mud (Hab = 3), helophyte (Hab = 4), gravel (Hab = 5), block (Hab = 6), pebble (Hab
168 = 7), root (Hab = 8), litter (Hab = 9), hydrophyte (Hab = 10) and bryophyte (Hab = 11). Each substrate
169 type was a priori ranked in relation to its ability to host organisms using “habitability” score (MEDAD,
170 2007). Based on this, percentage cover of low potential habitats were defined as the sum of
171 substrate types having a score ≤ 5 while percentage cover of high potential habitats were defined as
172 the sum of substrate types having a score ≥ 6.

173 **2.4. Water quality, hydrological and land cover variables**

174 In addition to terrestrial and aquatic habitat variables, we used three set of three a priori biologically
175 important regional drivers for benthic macroinvertebrates measured at each riverbank site (Table 1).
176 Water quality variables, i.e., conductivity (μS/cm) and temperature (degrees Celsius) measured using
177 the WTW 340i - TetraCon® 325 and dissolved oxygen (mg/L) measured using the Hach HQ30D.
178 Hydrological variables, i.e., stream width (m) assessed using a laser rangefinder and watershed area
179 (km²) and slope gradient (m/km) derived from Digital Elevation Model analysis, by calculating flow

180 direction grids and then delimiting individual drainage areas for each site along river networks with
181 the GRASS GIS software (GRASS Development Team, 2017). Land cover variables (Bissardon et al.,
182 1997), i.e., forest, agricultural and urban area proportions in the surrounding landscape measured
183 within a 500-m-radius around each riverbank site with the QGIS software (QGIS Development Team,
184 2015).

185 **2.5. Statistical analyses**

186 Analyses were performed with the R version 3.5.1 software (R Core Team, 2019).

187 For each set of independent continuous variables we built a synthetic latent variable using values of
188 the first axis of a principal component analysis (PCA). This PCA axis represented variations from low
189 to high vegetation density for terrestrial habitat variables, from low to high habitat quality for
190 aquatic habitat variables, from high to low water quality for water quality variables, from large to
191 small rivers for hydrological variables and from urban dominated to agricultural dominated
192 landscapes for land cover variables (Fig. A.3.). Because it appears more logical for water quality to
193 represent variations from low to high quality, values of the PCA first axis were reversed. We then test
194 if latent variables varied significantly among the five categories of riverbank sites using one-ways
195 ANOVAs with Tukey's post hoc tests. Finally, to explore the direct influence of riverbank protection
196 techniques on assemblage patterns, we created an ordinal variable that combined the effect of
197 technique with the age of the structure (named "riverbank structure
198 "). Based on the few available studies (Cavaillé et al., 2018; Li et al., 2006; Sudduth and Meyer, 2006),
199 riverbank protection techniques were ranked from low to high habitat quality (i.e., riprap -> mixed ->
200 crib wall -> fascine -> natural), and recent structures (i.e., 3 years old) were considered to have lower
201 habitat quality than did older ones (i.e., 9 years old). The resulting ordinal variable ranged from a
202 minimum value of 1, for 3-year-old riprap protection, to a maximum value of 19, for natural
203 riverbanks (see the column "Score" in Table A.1.).

204 To determine whether the taxonomic and functional composition of benthic macroinvertebrates
205 were shaped by the riverbank structure ordinal variable as well as by terrestrial habitat, aquatic

206 habitat, water quality, hydrological and land cover latent variables, we used multivariate generalized
207 linear models (mvabund package, Wang et al., 2012). We fitted the full model to each family and
208 feeding groups of benthic invertebrates that were present in > 10 % of the studied sites, and
209 summed across the univariate response to estimate their multivariate response with a negative
210 binomial distribution. The significance of independent variables in the multivariate GLM was
211 assessed using an analysis of variance with the PIT-trap method and 999 bootstrap resamples
212 (Warton et al., 2017). Moreover, to determine which family and feeding group best contribute to the
213 overall model deviance, we calculated univariate test statistics and p-values, adjusted to correct for
214 multiple testing (Holm's step-down procedure), for each family/feeding group (Wang et al., 2012).
215 Finally, to provide a graphical representation of the variation in family/feeding groups composition,
216 we used a canonical analysis of principal coordinates (Anderson and Willis, 2003), with a Bray-Curtis
217 distance.

218 To determine whether diversity patterns of benthic macroinvertebrates were influenced by the
219 riverbank structure ordinal variable as well as by terrestrial habitat, aquatic habitat, water quality,
220 hydrological and land cover latent variables, we used structural equation modelling (piecewiseSEM
221 package, Lefcheck, 2016). This was done to jointly test the direct and indirect effect of soil
222 bioengineering techniques on diversity patterns, while controlling for *a priori* important drivers of
223 benthic macroinvertebrates. Using literature review based on empirical data, we built an *a priori*
224 model that was expected to be the most plausible causal structure in explaining diversity patterns,
225 while keeping in mind that the ratio of the total number of samples to the number of variables
226 should not fall below 5 (Grace et al., 2015). Our model hypothesized that local terrestrial and aquatic
227 habitat quality latent variables would mediate the indirect effect of the type of riverbank structure
228 on benthic macroinvertebrates; and that water quality, hydrological and land cover latent variables
229 would directly influence diversity patterns. We fit the same *a priori* model structure to four
230 dependent variables, i.e., native, exotic, shredder and scraper taxa, and used a Gaussian distribution
231 to model the relationship between both terrestrial and aquatic habitat latent variables and the

232 riverbank structure ordinal variable. To model the relationship between native, exotic, shredder and
233 scraper taxa and local and regional drivers we used a Poisson distribution for richness and a Negative
234 Binomial distribution for abundance. The goodness-of-fit of the model was assessed using Fisher's C
235 statistic and a test of directed separation, while the variance explained was estimated using the
236 coefficient of determination. Finally, because part of the model relied on GLMs, the results report
237 only unstandardized coefficients.

238

239 **3. Results**

240 Overall, 94 benthic macroinvertebrate families were recorded on the 37 riverbank sites for a total of
241 80,500 individuals collected. Richness averaged 26 families per site ($SD \pm 9.8$), with a range of 7-49
242 families, while abundance averaged 2,176 individuals per site ($SD \pm 1,633$), with a range of 55-6,141
243 individuals.

244 One-way ANOVA revealed that only terrestrial ($p = 0.000$) and aquatic ($p = 0.001$) habitat variables
245 varied significantly among riverbank protection techniques (Fig. 2). Tukey HSD test showed that the
246 density of riparian vegetation was significantly more important on mixed, crib wall and fascine
247 structures as compared to riprap structures and natural sites and that the quality of aquatic habitat
248 was significantly higher on fascine structures and natural sites as compared to riprap and mixed
249 structures (Fig. 2).

250 **3.1. Composition of benthic macroinvertebrates communities**

251 For the taxonomic approach, multivariate GLMs showed that family composition was not influenced
252 by the riverbank structure ordinal variable ($Dev = 87$, $p = 0.157$), nor by terrestrial habitat ($Dev = 55$,
253 $p = 0.530$), aquatic habitat ($Dev = 83$, $p = 0.233$), water quality ($Dev = 98$, $p = 0.146$), hydrological
254 ($Dev = 158$, $p = 0.140$) or land cover ($Dev = 245$, $p = 0.100$) latent variables. Based on the deviance
255 explained by individual parameters it appears however clear that most of the variation in family
256 composition was related to differences in land cover composition, quite well represented by the
257 second CAP axis (Fig. 3.A), and hydrological contexts among riverbank sites, which is well

258 represented by the first CAP axis. Univariate tests for each family revealed that none of them was
259 significantly related to the parameters tested (Table A.4.).

260 For the functional approach, multivariate GLMs showed that feeding habit composition was
261 significantly influenced by aquatic habitat (Dev = 23, $p = 0.039$), hydrological (Dev = 66, $p = 0.001$)
262 and land cover (Dev = 32, $p = 0.008$) latent variables. The riverbank structure ordinal variable (Dev =
263 10, $p = 0.391$) as well as the terrestrial habitat (Dev = 7, $p = 0.551$) and water quality (Dev = 11, $p =$
264 0.280) latent variables had no significant effect. Based on the deviance explained by individual
265 parameters, most of the variation in feeding groups was related to differences in hydrological
266 contexts among riverbank sites, which is well illustrated by the first CAP axis (Fig. 3.B). Univariate
267 tests for each feeding habit group revealed that scrapers (Dev = 30.8, $P_{adj} = 0.001$), shredders (Dev =
268 17.8, $P_{adj} = 0.003$) and predators (Dev = 10.7, $P_{adj} = 0.022$) were significantly related to variations in
269 hydrological context among riverbank sites and that deposit-feeders (Dev = 13.1, $P_{adj} = 0.018$) and
270 piercers (Dev = 8.3, $P_{adj} = 0.046$) were significantly related to variations in aquatic habitat quality
271 among riverbank sites (Table A.5.). As a consequence, divergence in functional composition was
272 mostly due to the largest abundance of scrapers, shredders and predators along small size rivers and
273 to the largest abundance of deposit-feeders and piercers along banks dominated by low potential
274 aquatic habitats.

275 **3.2. Diversity of benthic macroinvertebrates communities**

276 The *a priori* structural equation model was well suited for the data (Fisher's $C = 8.99$, $df = 14$, $p =$
277 0.832) and all component of the model jointly explained 20% to 90% of the variations in benthic
278 macroinvertebrate richness and abundance (Fig. 4). This *a priori* model also explained quite
279 significant variation in riparian vegetation density ($R^2 = 17\%$) and aquatic habitat quality ($R^2 = 36\%$) as
280 a function of riverbank structure. For native taxa, richness and abundance increased from urban
281 dominated to agricultural dominated landscapes and from large to small rivers, only abundance
282 increased from low to high water quality while only richness increased from civil engineered to soil
283 bioengineered structures. For exotic taxa, only richness decreased from large to small rivers and from

284 high to low water quality, while none of the parameters influenced abundance patterns. For
285 shredders, richness and abundance increased from urban dominated to agricultural dominated
286 landscapes and from large to small rivers, while only richness increased from civil engineered to soil
287 bioengineered structures. For scrapers, richness and abundance increased from urban dominated to
288 agricultural dominated landscapes and from large to small rivers, while only abundance increased
289 from low to high water quality.

290

291 **4. Discussion**

292 Our results clearly showed that benthic macroinvertebrate assemblages were more influenced by
293 regional than by local drivers. Although we have found evidences that soil bioengineering improve
294 terrestrial and aquatic habitat conditions and benefit to benthic macroinvertebrates, the hydrological
295 context, land cover composition and, to a lower extent, water quality conditions performed much
296 better in explaining variations in composition and diversity. Along river networks, catchment-scale
297 properties and landscape attributes surrounding riverbank sites appeared to be major drivers of
298 benthic macroinvertebrate assemblages. To achieve ecological improvement, river practitioners and
299 managers should therefore take into account the hierarchical structure of the regional and local
300 drivers in designing and implementing restoration operations.

301 **Soil bioengineering improves local habitat conditions and benefit to benthic macroinvertebrates**

302 As expected, both terrestrial and aquatic habitat qualities increased along riverbanks stabilized with
303 soil bioengineering techniques, specifically for stabilization structures made of willow fascines and
304 vegetated crib wall (Fig. 2). Given that soil bioengineering consists in integrating vegetation into
305 engineering design (Evette et al., 2009), the increase in vegetation density reported herein reflects
306 the fact that pure bioengineering techniques used a higher proportion of plant material and may also
307 better promote the recruitment and growth of plant species along stabilized riverbanks (Li et al.,
308 2006; Schmitt et al., 2018). Moreover, we showed that the immersed part of the riverbank benefited
309 from these nature-based solutions. Thus, when comparing soil bioengineering structures to mixed

310 and civil engineering structures, an increase in the proportion of high potential habitats for
311 macroinvertebrates was highlighted. Even more, we found that the quality of aquatic habitat was
312 quite similar between willow fascine structures and natural willow stands (Fig. 2). As reported in
313 other studies (Li et al., 2006; Pander et al., 2017; Sudduth and Meyer, 2006), our results confirm that
314 the introduction of tree species to stabilize riverbanks could benefit instream habitats by e.g.,
315 fostering the development of fine root systems and the inputs of woody debris and leaf litter into the
316 rivers. However, restoration efforts relying on replanting strategies only (Giling et al., 2015; Parkyn et
317 al., 2003) and/or stabilization structures using riprap at the lower submerged part (Cooperman et al.,
318 2007; Schmitt et al., 2018) have been showed to be of low ecological value for freshwater
319 communities. In accordance, we found that mixed and riprap structures induced an increase in the
320 proportion of low potential habitats for macroinvertebrates (e.g., slab). To foster the ecological
321 benefit of stabilization structures along riverbanks, it therefore appears essential to promote
322 substrate heterogeneity deeper in the aquatic environment and to avoid, whenever possible,
323 submerged bank protection dominated by ripraps (e.g., Schmitt et al., 2018).

324 Related changes in aquatic habitat conditions influenced the composition of macroinvertebrate
325 feeding groups. Even though the deviance explained by the aquatic habitat variable was lower than
326 the one explained by regional drivers, a significant effect was found. Specifically, we showed that
327 deposit-feeders and, to lower extend, piercers were more abundant along banks dominated by low
328 potential aquatic habitats. This may underlines thicker layers of fine detrital organic matter that
329 settle out and accumulate between the rock blocs of riprap and mixed stabilization structures (Feld
330 and Hering, 2007). However, despite the fact that numerous studies have established a clear link
331 between aquatic habitat quality and macroinvertebrate diversity (Buffagni et al., 2019; Coggerino et
332 al., 1995; Li et al., 2018; Verdonschot et al., 2016), in the foothills of the Alps and Jura Mountains,
333 diversity patterns were not influenced by local terrestrial and aquatic habitat conditions. Instead, we
334 found that the richness of natives and shredders increased from civil engineered to soil
335 bioengineered stabilization structures (i.e., with direct increasing value of the riverbank structure

336 ordinal variable). This suggests that beyond changes in riparian vegetation density and in the
337 proportion of high potential habitats, soil bioengineering induces other changes in local abiotic
338 conditions which benefit to overall benthic macroinvertebrates as well as specialized species, i.e.,
339 relying on coarse particulate of organic matter. Especially, we argued that willow fascines and
340 vegetated crib wall increase resource input of coarse organic material (i.e., woody debris, leaves,
341 roots) at the reach-scale in a manner comparable to that of natural willow stands, which directly
342 benefit to shredders (Cummins et al., 1989; Turunen et al., 2019). More generally, we inferred that
343 the introduction of tree species to stabilize riverbanks increases shade over parts of the river,
344 preventing thus the heating of water (Dugdale et al., 2018; Garner et al., 2017), and increases
345 biophysical interactions with water and sediment flows, enhancing thus the trapping of sediments,
346 organic matter and nutrients and favouring the development of additional fluvial landforms
347 (Corenblit et al., 2007; Hortobágyi et al., 2018). These changes in environmental conditions, if they
348 occur over a river segment embedded in a landscape dominated by low riparian habitat quality, may
349 be very attractive for macroinvertebrate populations and foster the co-occurrence of various taxa at
350 local scale. Thus, in accordance with the few available studies (Cavaillé et al., 2018; Pander et al.,
351 2017; Sudduth and Meyer, 2006), our results pointed out that soil bioengineering can be a good
352 compromise solution to support both erosion control and freshwater communities. However, the
353 ecological benefits of these nature-based solutions should be rationalized, as it appears clear that the
354 improvement of riparian habitat quality induces by soil bioengineering alone cannot solve
355 environmental degradations due to human activities in surrounding landscape.

356 **Regional drivers primarily shape benthic macroinvertebrate assemblages**

357 Consistently with studies that have investigated the relative influence of multiple scale drivers on
358 benthic macroinvertebrates (Bruno et al., 2014; Feld and Hering, 2007; Heino et al., 2003; Townsend
359 et al., 2003), we found that composition and diversity patterns were more strongly explained by
360 regional than by local drivers. Specifically, we highlighted that the hydrological context, i.e., a
361 variable combining stream width, watershed area and slope gradient, best explained

362 macroinvertebrate assemblages (Townsend et al., 2003). Thus, in accordance with the river
363 continuum concept (Vannote et al., 1980), the composition of taxa feeding habits was structured in a
364 predictable manner, i.e., communities dominated by scrapers, shredders and predators were located
365 along small headwaters streams. Thanks to the structural equation modelling approach, which allows
366 balancing the relative importance of parameters in models, it appears clear that changes in
367 communities structure was firstly due to the larger abundance of scrapers and shredders taxa in
368 small streams, secondly to their larger richness. Due to close relationship between taxa abundance
369 and resource availability, framed within the species-energy hypothesis (Wright, 1983), this may
370 confirms the leading role played by organic materials in shaping benthic macroinvertebrate
371 communities (Vannote et al., 1980). Also, contrary to empirical evidences (Heino et al., 2003;
372 Minshall et al., 1985; Paller et al., 2006), we found that total richness of native taxa decreased with
373 increasing river size. The river continuum concept predicts that biotic diversity increases with stream
374 size, reaching maximum values in midreaches and then decreasing in very large rivers (Vannote et al.,
375 1980). However, this biodiversity-stream size relationships has been showed to be rather weak,
376 especially for macroinvertebrate communities (Vander Vorste et al., 2017). Moreover, because
377 stream size correlates well with a large number of other variables, a mechanistic explanation is
378 needed to disentangle the drivers controlling biodiversity in riverine ecosystems (Vander Vorste et
379 al., 2017). In this regard, our results also showed that the richness of exotic taxa increased from small
380 to large rivers. Beyond the confirmation that exotic taxa benefit from more connected river networks
381 (Leuven et al., 2009), those results give evidence that the biodiversity-stream size relationships
382 should not be investigated based solely on synthetic metrics of diversity, such as total richness. We
383 thus inferred that the pattern observed can be attributed to a combination of multi-stressors,
384 probably linked to the fact that largest rivers in our study area are more likely to be subject to
385 channeling, which induces physicochemical and morphological degradations to the benefit of exotic
386 taxa (Früh et al., 2012) and to the detriment of native taxa.

387 Beside the influence of the hydrological context, it has been shown that the landscape attributes
388 surrounding the riverbanks strongly influence benthic macroinvertebrates communities (Lorenz and
389 Feld, 2013). Thus, land cover explained most of the variation in the taxonomic composition, even
390 though not significant, and ranked second in explaining variation in the functional composition. In
391 addition, richness and abundance of native, scraper and shredder taxa increased with a decreased
392 proportion of urban dominated landscapes. This confirms the substantial effect that human
393 infrastructures have in the direct vicinity of rivers on benthic macroinvertebrates (Feld and Hering,
394 2007; Kail and Wolter, 2013; Moore and Palmer, 2005; Roy et al., 2003). Indeed, by increasing built-
395 up areas around rivers, human activities can alter riparian habitat quality (e.g., by reducing the width
396 of the forest buffer) and water properties (e.g., by increasing organic pollution, acidity and turbidity)
397 (King et al., 2005). However, contrary to close linkages established between urban land cover and
398 water quality, and related negative effects on the diversity of benthic macroinvertebrates (Roy et al.,
399 2003), in our study area, land cover and water quality were independent (i.e., the test of directed
400 separation was not significant). This may underline the fact that most of the riverbanks studied were
401 embedded in an agricultural dominated landscape (see Table 1), with only 9 riverbank sites having
402 more than 50 % of urban areas in the surrounding landscape. Thus, when comparing the relative
403 influence of land cover and water quality drivers on benthic macroinvertebrate assemblages, we
404 found less direct influence for the latter. Indeed, only the abundance of scraper and native taxa
405 increased with increasing value of water quality, while the richness of exotic taxa decreased. This
406 result may be linked to the higher success of non-native benthic macroinvertebrates with increased
407 loads of pollutants as it has already been observed (Früh et al., 2012). Also, these opposite patterns
408 give weight to the view that exotic taxa share different traits than native taxa, i.e., they are mostly
409 collector-filterers, belong to the molluscs or crustaceans taxonomic groups, and are more tolerant to
410 organic pollution (Karatayev et al., 2009). Overall, our results highlight the hierarchical structure of
411 the regional drivers on macroinvertebrates and confirm the importance of considering multiple scale

412 parameters for a better understanding of the structure of freshwater communities (Bruno et al.,
413 2014; Feld and Hering, 2007; Heino et al., 2003; Kail and Wolter, 2013).

414

415 **5. Conclusions**

416 The response of freshwater communities to instream habitat restoration has been shown to be
417 inconsistent (Palmer et al., 2010). As opposed to terrestrial biodiversity, which benefits more strongly
418 from local restoration efforts, the recovery of aquatic biodiversity remains largely under the control
419 of large-scale stressors, which prevent taxa recolonization (Pilotto et al., 2019). As such, the few
420 previous studies that have investigated the response of fish and benthic macroinvertebrate
421 communities to soil bioengineering have found either a positive significant effect (Cavaillé et al.,
422 2018; Dolph et al., 2015; Pander et al., 2017; Sudduth and Meyer, 2006) or a non-significant effect
423 (Cooperman et al., 2007; Ernst et al., 2012; Schmitt et al., 2018; Selvakumar et al., 2010). By moving
424 beyond simple categories of individual riverbank stabilization structures and by accounting for local
425 and regional potential important abiotic drivers, we showed that soil bioengineering has a positive
426 effect on benthic macroinvertebrates. However, as compared to regional drivers, especially
427 catchment-scale properties and landscape attributes, local drivers were of lower importance in
428 shaping macroinvertebrate assemblages. Thus, if stabilization structures are implemented with the
429 aim both of controlling erosion and of improving ecological properties of riverbanks for aquatic
430 biodiversity, the potential impact of large scales anthropogenic pressures on ecological restoration
431 success should be addressed as soon as possible (Kail and Wolter, 2013; Pilotto et al., 2019). Finally,
432 from an operational point of view, our results suggest that the ecological benefits of soil
433 bioengineering for freshwater communities can be maximized along small size rivers embedded in an
434 agricultural dominated landscape.

435

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442

443 **7. References**

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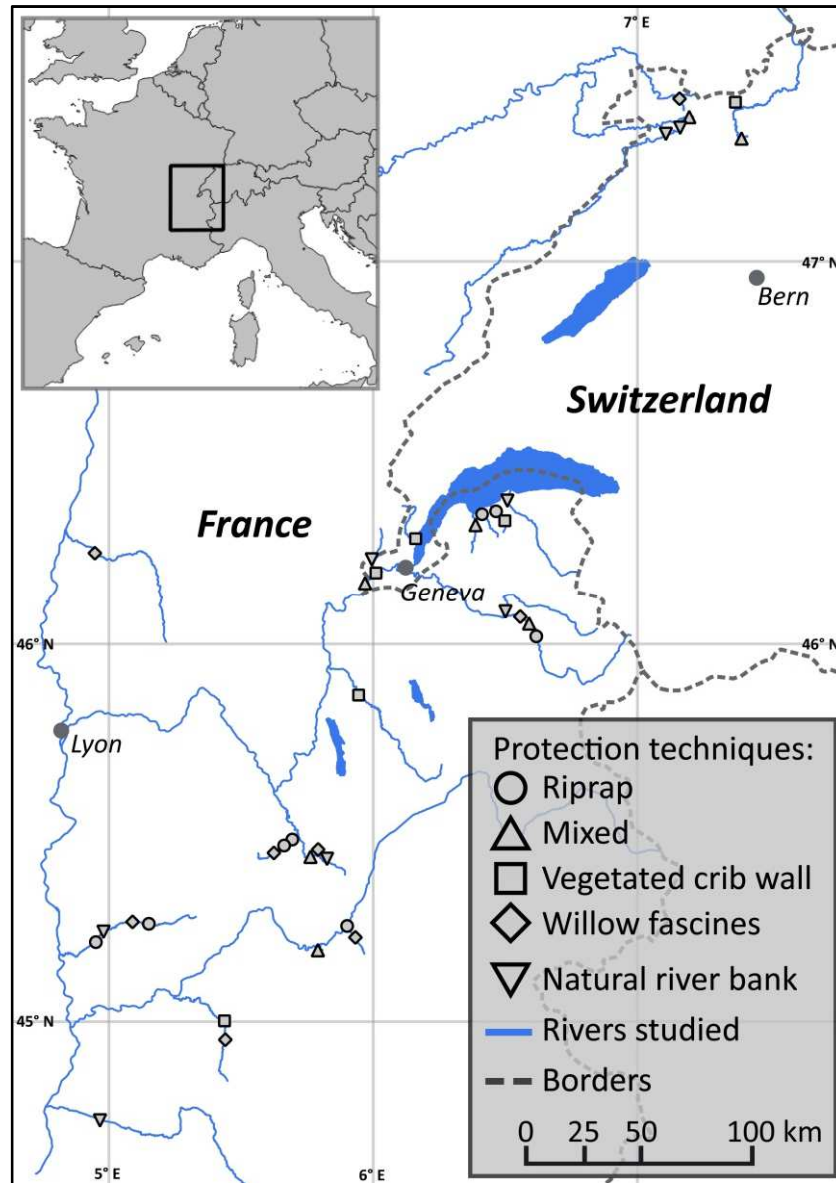
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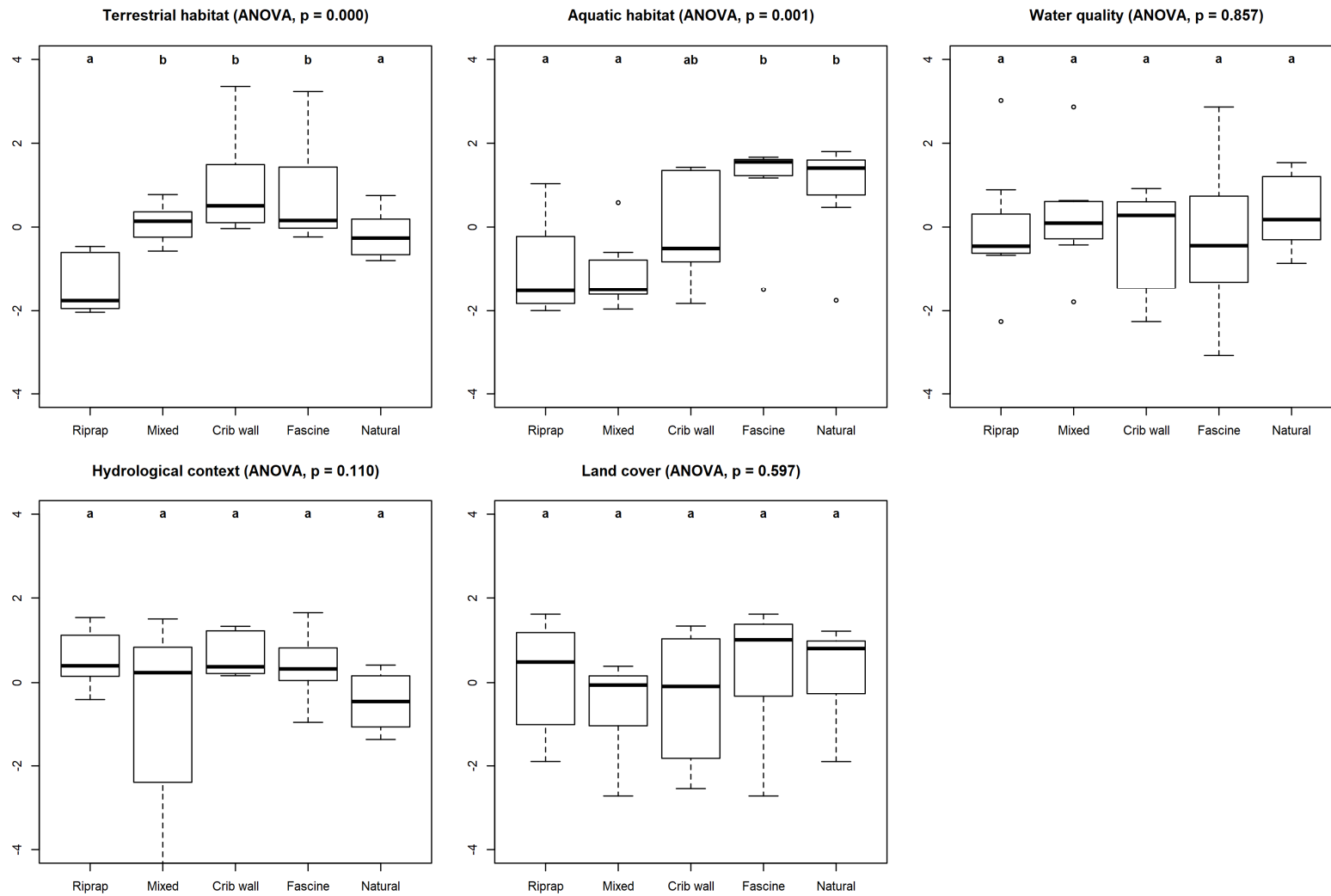
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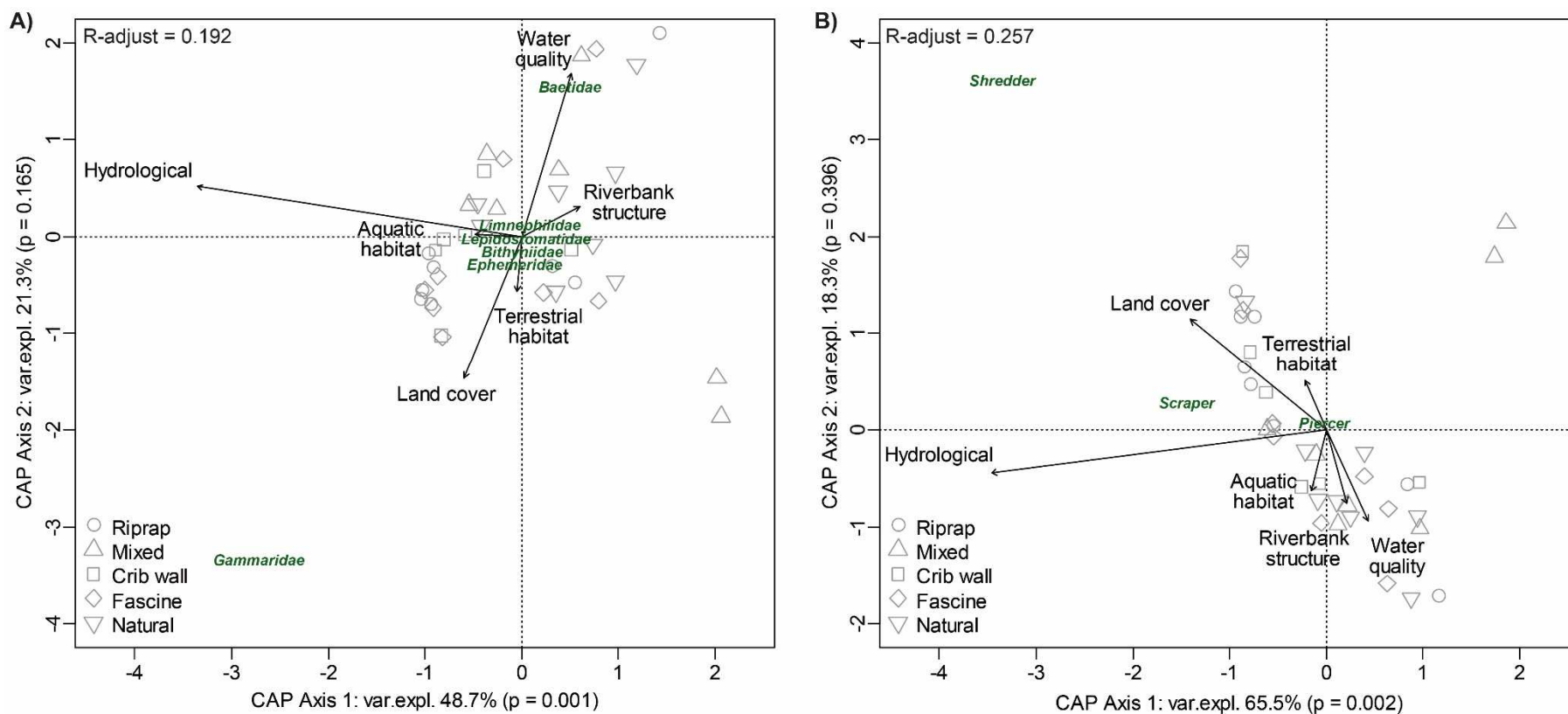
661 **Fig. 1.** Study area and distribution of rivers and sites sampled for riverbank protection techniques in
662 the foothills of the Alps and Jura Mountains (France and Switzerland).



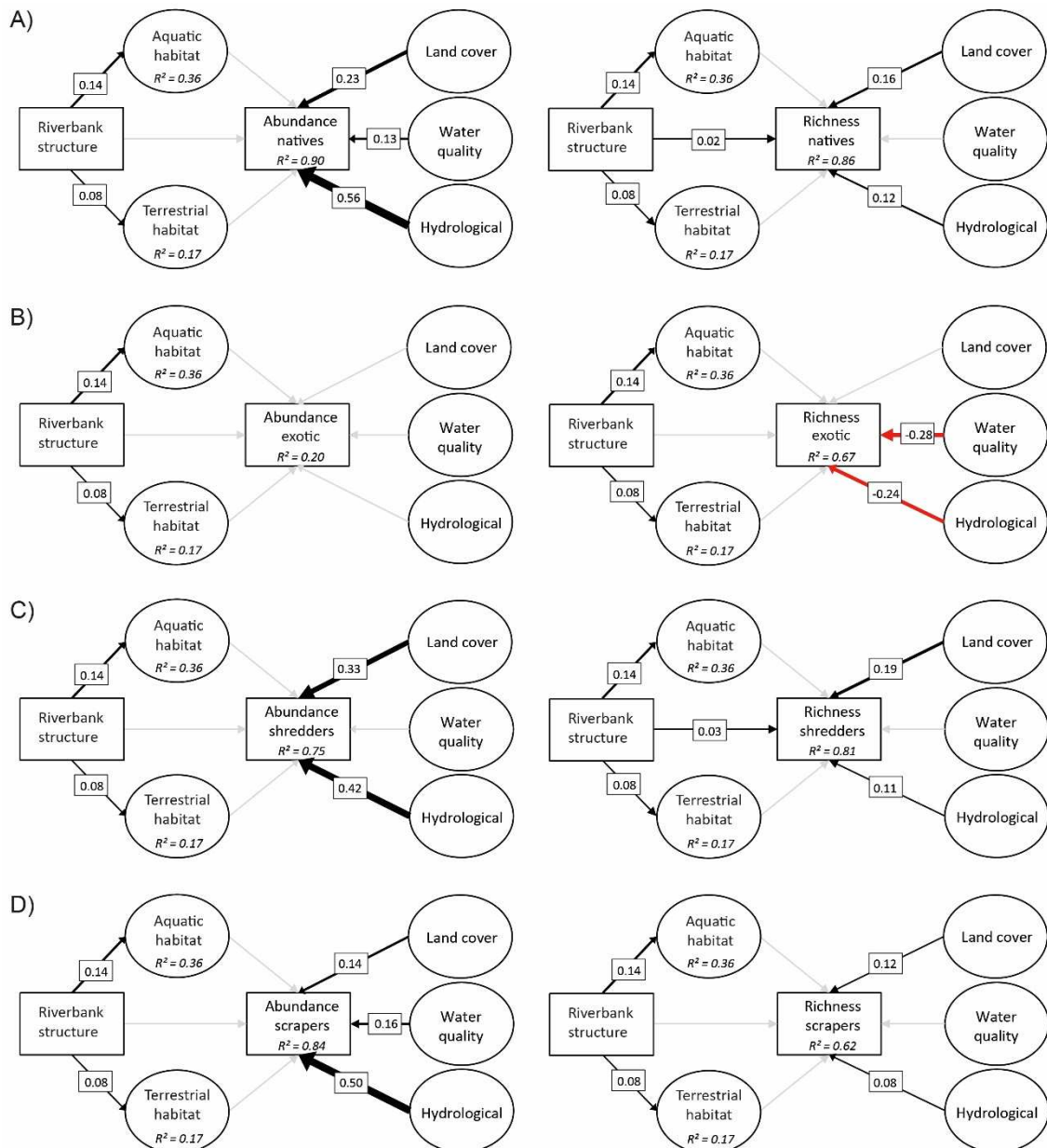
663 **Fig. 2.** Boxplots showing variations in terrestrial habitat, aquatic habitat, water quality, hydrological context and land cover latent variables in relation to
664 riverbank protection techniques factor in the foothills of the Alps and Jura Mountains (France and Switzerland). Bold letters indicate significance differences
665 ($p < 0.05$) between factor levels based on Tukey's HSD post hoc test.



666 **Fig. 3.** Constrained canonical analysis of principal coordinates of A) family and B) feeding groups of benthic macroinvertebrates in relation to the riverbank
 667 structure ordinal variable as well as the terrestrial habitat, aquatic habitat, water quality, hydrological and land cover latent variables, in the foothills of the
 668 Alps and Jura Mountains (France and Switzerland). To facilitate graphical interpretation, the most influential family and feeding groups, i.e., the ones that
 669 had a cumulated deviance > 20 are represented (see also Table A.4. & A.5.).



670 **Fig. 4.** Structural equation models exploring the relationships among the riverbank structure ordinal
 671 variable, terrestrial habitat, aquatic habitat, water quality, hydrological and land cover latent
 672 variables and richness and abundance of A) native, B) exotic, C) shredder and D) scraper benthic
 673 macroinvertebrates. Arrows represent unidirectional relationships among variables. Black arrows
 674 denote positive relationships, red arrows negatives, grey arrows non-significant paths. The thickness
 675 of the significant paths has been scaled based on the magnitude of the unstandardized regression
 676 coefficient, given in the associated box. Pseudo- R^2 for component models is given in the boxes of
 677 response variables.



678 **Table 1.** Description of environmental variables used to model assemblage patterns of benthic
679 macroinvertebrates along different riverbank structures, plus natural riparian willow stands, in the
680 foothills of the Alps and Jura Mountains (France and Switzerland).

Variables	Description	mean (\pm SD)	Range
Local drivers			
Terrestrial habitat variables:			
Dens_Herb	Density of herbaceous species	146.92 (\pm 71.99)	26.00 - 408.00
Dens_Lign	Density of ligneous species	100.73 (\pm 68.78)	4.00 - 306.00
Dens_Exot	Density of exotic plant species	11.97 (\pm 17.25)	0.00 - 86.00
Aquatic habitat variables:			
Rich_Habit	Richness of habitats	5.81 (\pm 1.71)	3.00 - 11.00
Prop_LowQ	Low quality habitat proportion (%)	49.00 (\pm 38.03)	1.00 - 98.00
Pro_HighQ	High quality habitat proportion (%)	51.00 (\pm 38.03)	2.00 - 99.00
Regional drivers			
Water quality variables:			
Temperature	Water temperature ($^{\circ}$ C)	13.19 (\pm 2.59)	7.20 - 19.10
Conductivity	Water conductivity (μ S/cm)	460 (\pm 177)	240 - 990
Oxygene	Dissolved oxygen in water (mg/L)	10.63 (\pm 0.83)	8.86 - 13.05
Hydrological context variables:			

Stream_W	Stream width (m)	20.29 (± 23.12)	3.00 - 107.00
Watershed	Watershed area (km ²)	68.86 (± 186.34)	0.44 - 1,006
Slope	Longitudinal slope of the river (m/km)	84.30 (± 69.23)	3.80 - 249.11
Land cover composition variables:			
Prop_Forest	Forest proportion (% , 500-m-radius)	24.98 (± 23.42)	0.00 - 89.02
Prop_Urban	Urban area proportion (% , 500-m-radius)	28.54 (± 33.38)	0.00 - 100
Prop_Agri	Agricultural area proportion (% , 500-m-radius)	45.07 (± 31.32)	0.00 - 100

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