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1 **Diversity and succession of riparian plant communities along riverbanks**
2 **bioengineered for erosion control: a case study in the foothills of the Alps and the**
3 **Jura Mountains**

4

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23

24 **Highlights**

- 25 - Bioengineering enhanced plant species richness and cover, compared to ripraps
- 26 - Over time, bioengineering favored shade-tolerant and competitive species
- 27 - Plant communities in ripraps changed little along a 14-year chronosequence
- 28 - Engineer species as *Salix* triggered vegetation succession in stabilization projects

29

30 **Abstract**

31 Soil bioengineering for riverbank stabilization involves the use of living plant materials
32 to treat unstable or eroding riverbanks. These near-natural structures may harbor a
33 higher plant richness and vegetation cover compared to classical civil engineering
34 structures such as ripraps, but little information exists on vegetation dynamics during
35 secondary succession on stabilized riverbanks. We hypothesized that soil
36 bioengineering, by means of active introduction of early successional *Salix* shrubs, can
37 foster successional trajectories of riparian plant communities, unlike civil engineering.
38 We sampled three types of riverbank stabilization structures: pure bioengineering
39 structures, mixed structures (combining riprap and bioengineering techniques) and
40 ripraps, across a 14-year sequence on 42 sites located along 23 different streams running
41 through the foothills of the Alps and the Jura Mountains (France and Switzerland). We

42 quantified species richness and density and compared the temporal patterns of four
43 groups of species that normally appear sequentially in natural succession on riverbanks
44 (ruderal, hygrophilous, shade-tolerant, competitive species), as well as non-native
45 species. Plant community composition differed greatly between ripraps and the two
46 types of bioengineered sites, and ligneous species typical of advanced successional
47 stages (*Cornus sanguinea*, *Corylus avellana*) spontaneously established in the oldest
48 bioengineered sites. In general, richness of total species was higher in stabilization
49 structures using soil bioengineering (including mixed structures) than in riprapped sites.
50 In particular, the number of shade-tolerant and competitive species in bioengineered
51 sites was double that found at ripraps after 14 years. Yet, richness of shade-tolerant
52 species increased over time only on purely bioengineered sites, and their density there
53 was almost twice that in mixed structures. Neither the type of stabilization structure nor
54 time explained the variability in richness and density of non-native species across sites.
55 Our study showed that along streams running through foothills, where erosion processes
56 are usually intense, vegetation of bioengineered riverbanks exhibits successional
57 dynamics similar to those theoretically found in natural conditions. Bioengineering can
58 therefore foster ecological processes while stabilizing eroding riverbanks along foothill
59 streams, thus satisfying human needs for infrastructure protection with less impact on
60 the riparian ecosystem than riprap structures.

61 **Keywords**

62 Bioengineering; Mixed techniques; Ripraps; Riverbank stabilization; Vegetation
63 succession; Willow fascines

64 **1. Introduction**

65 Most streams and associated riparian zones worldwide have been altered by ‘hard’ civil
66 engineering structures such as dams, weirs, levees, dikes and other erosion protection
67 structures. These structures are needed to control flooding and prevent channel
68 migration in the presence of agriculture or urban and transport infrastructures in
69 floodplains, but at the same time they drastically modify natural river dynamics (Feld et
70 al., 2011; Nilsson et al., 2005). Associated changes in abiotic and biotic conditions
71 including water quality have resulted in several directives to stimulate stream
72 restoration in Europe, notably the Floods Directive of 2007, the European Water
73 Framework Directive of 2000, and the Habitat Directive of 1992 (Gumiero et al., 2013;
74 Carvalho et al., 2019). In that regard, recent literature reviews revealed that restoration
75 actions that modify the prevalent water and/or sediment regime are increasingly and
76 efficiently used to restore riparian vegetation, for example, by operating dams to satisfy
77 plant requirements, or by removing or relocating levees and dikes (González et al.,
78 2015; 2018). Yet, such restoration strategies could conflict with the human
79 infrastructures in close proximity. Where erosion control is of primary concern to
80 ensure public safety, soil bioengineering could represent a good compromise between
81 civil engineering and ecological restoration.

82 Soil bioengineering is in fact often viewed as riparian ecosystem restoration, *sensu lato*,
83 because it promotes the recruitment and growth of native plant species along stabilized
84 riverbanks (Li et al., 2006) and, more generally, because it facilitates the partial
85 recovery of some of the main ecological functions previously provided by now
86 degraded riverbanks, i.e. biodiversity support, ecological corridor, and decontamination
87 (Karle and Densmore, 1994; Sudduth and Meyer, 2006). As a nature-based solution,

88 soil bioengineering uses the physical properties of living plants to minimize the
89 negative impacts of artificial bank stabilization on stream ecosystems (Rey et al., 2019).
90 It has been used for centuries in Europe (Evette et al., 2009) and consists in copying
91 natural systems by integrating vegetation into engineering design in order to protect hill
92 slopes, embankments and human structures from erosion and other undesired
93 geomorphological processes (e.g., sediment deposition, channel incision and channel
94 migration; Gray and Sotir, 1996; Shields et al., 2008). The positive effects of soil
95 bioengineering on riparian habitats in terms of biodiversity support (fishes,
96 macroinvertebrates) have been empirically demonstrated by several studies (Sudduth
97 and Meyer, 2006; Cavaillé et al., 2018; Schmitt et al., 2018; Janssen et al., 2019).
98 However, the effects on plant biodiversity itself have received less attention (but see
99 Cavaillé et al., 2013; Schmitt et al., 2018). In particular, it is not known whether the
100 successional dynamics of plant communities on bioengineered banks resemble those of
101 natural riverbanks. Yet, knowing the ability of these nature-based solutions to initiate
102 vegetation succession is essential to assess whether they meet the self-organization
103 requirement necessary to declare full recovery in restoration projects (see International
104 principles and standards for the practice of ecological restoration in Gann et al., 2019).

105 Plant communities in riparian areas are mostly shaped by flood disturbance: species
106 associated with early stages of riparian succession frequently encounter physical and
107 physiological constraints such as anoxia, shear stress or submersion, rather than limited
108 light and plant competition, as in later stages of succession (Corenblit et al., 2007,
109 2015). The first phases of succession in riparian systems are typically characterized by
110 the colonization of pioneer species like willows, poplars/cottonwoods, and herbaceous
111 species with ruderal, light-demanding, short-lived characteristics and affinity for hydric

112 conditions (McCoy-Sulentic et al., 2017; Muñoz-Mas et al., 2017). As succession
113 advances and fluvial landforms age, aggrade and disconnect from the stream channel,
114 flooding disturbance is replaced by inter-specific interactions (e.g., competition,
115 facilitation) as the main driver of vegetation change (Tabacchi et al., 1998; 2019).
116 According to the passive relay floristic approach (i.e. Field of Dreams hypothesis *sensu*
117 Palmer et al., 1997), the active introduction of early successional woody species, such
118 as *Salix* spp. (willows), which are also ecosystem engineer species (Gurnell, 2014),
119 should affect the riverbank physical environment and foster the development of plant
120 communities during secondary succession (Lennox et al., 2011; McClain et al., 2011).
121 Active revegetation may be seen as an “assisted” succession for the over- and
122 understory composition of riparian vegetation. It is a common practice in invasive
123 species management projects following the removal of undesired plants (González et
124 al., 2017b; Ruwanza et al., 2013) or after abandonment of agriculture in the floodplain,
125 when a limited inflow of propagules occurs (Battaglia et al., 2002; Bunting et al., 2013;
126 Bourgeois et al., 2016). Active revegetation by seeding or planting cuttings (or stakes)
127 helps recruit other native and typically riparian species, with different techniques
128 leading to different plant communities (Van Looy et al., 2011). In riparian areas
129 stabilized by soil bioengineering techniques, shrubs are frequently assembled into
130 fascines or brushlayers, which consist respectively of branches tied together in linear
131 cylindrical bundles or in multiple layers, placed on streambanks with or without a rock
132 embankment in the lower part of the bank, depending on local constraints (Li and
133 Eddleman, 2002). We suggest that such bioengineering practices also represent a type of
134 assisted succession. As is the case for active revegetation, different bioengineering
135 techniques have been shown to strongly influence the resulting plant community

136 (Cavaillé et al., 2013; Schmitt et al., 2018). To our knowledge, however, how
137 succession is modulated by bioengineering alone, i.e. "pure" bioengineering, or
138 combined with hard civil engineering, i.e. "mixed" bioengineering, has not been
139 reported in the scientific literature.

140 This study aimed to investigate if soil bioengineering can foster succession of riparian
141 plant communities through the active introduction of early successional shrub species
142 on riverbanks. Specifically, we examined how plant community composition varied
143 between sites where pure versus mixed soil bioengineering techniques were
144 implemented, and compared to sites with civil engineering stabilization structures of
145 different ages in the French and Swiss foothills of the Alps and the Jura Mountains.
146 Many soil bioengineering structures have been successfully applied to foothill streams
147 of these regions where bank erosion is an important issue in proximity to roads and
148 other infrastructure. We hypothesized that by adding pioneer engineer species, soil
149 bioengineering bypasses the natural establishment of pioneer and ruderal species, and
150 fosters a faster transition to a dominance by post-pioneer competitive species.
151 Conversely, we hypothesized that civil engineering facilitates the recruitment and
152 establishment of opportunistic (notably non-native) and fast-colonizing species and
153 leads to a different and slower successional trajectory than bioengineering. For
154 simplicity, the term bioengineering is used instead of soil bioengineering in the sections
155 below.

156

157 **2. Material and methods**

158 *2.1. Study area and sampling design*

159 The study area is located in the French and Swiss foothills of the Alps and the Jura
160 Mountains, within the Rhône River watershed (Figure 1). This region is characterized
161 by a limestone substratum and a temperate climate. We selected 23 streams, extending
162 between the Drôme River (44°43'N; 4°58'E) in the southern part of the study area and
163 the Doubs River (47°21'N; 7°10'E) in the northern part, at elevations ranging from 134
164 to 700 m a.s.l. All of the streams studied belong to the same vegetation zone, i.e.,
165 “lower and mid-mountain: collinean and montane vegetation belts” (Ozenda and Borel,
166 2000), and to the same major group of stream types in Europe, i.e., mountain streams
167 (Sandin and Verdonschot, 2006).

168 In 2011, 42 riverbank sites were sampled to assess the response of plant communities to
169 different types of engineered riverbank stabilization structures for erosion control over
170 time (a complete description of sampled sites, including year of completion, country,
171 river and absolute elevation, is provided in Appendix S1). We selected three types of
172 stabilization structures from among those most commonly used (Figure 2): “pure”
173 bioengineering protection (i.e. willow fascines on the lower part of the bank,
174 brushlayers and cuttings of willow species on the middle part and herbaceous seeding
175 on the upper part of the bank, 15 sites); “mixed” protection (i.e. a technique combining
176 hard civil engineering – riprap – on the lower part, brushlayers and cuttings of willow
177 species on the middle part and herbaceous seeding on the upper part, 13 sites); and
178 “riprap” protection (i.e. hard civil engineering protection on the entire bank, 14 sites).
179 Willow species used in bioengineering techniques (fascines and cuttings) were *Salix*
180 *viminalis* L., *S. purpurea* L., *S. triandra* L., *S. myrsinifolia* Salisb. and *S. pentandra* L.
181 We used a space-for-time substitution approach to construct a chronosequence of 14

182 years (the number of sites was distributed evenly across years and stabilization
183 structures, Appendix S1).

184 2.2. *Vegetation survey*

185 Riparian vegetation was sampled between May and July 2011 using the Line Point
186 Intercept method (Bonham, 1989) to detect the presence and frequency of occurrence
187 (i.e. density) of plant species. At each site, three 25-m transects (lower, middle, upper)
188 were set parallel to the stream channel. The lower transect was placed close to the water
189 line at low-flow discharge. The middle transect was placed at an elevation determined
190 according to the biannual flood recurrence water level, estimated visually using the
191 presence and occurrence of wetland species, signs of recent flooding disturbance (i.e.,
192 plant debris; bent branches) and the morphology of the channel. The upper transect was
193 placed near the edge of the riverbank and we assumed that it did not flood regularly. All
194 sites were sampled during low-flow conditions, so that transects near the low-flow
195 water level would be comparable across sites. At each transect, sampling points were
196 established every meter for a total of 75 points per site. At each sampling point, all plant
197 species intercepted by a vertical rod or its upward projection were recorded and
198 identified. All specimens were determined to the species level, except for *Rubus* spp.
199 and *Festuca* spp., which were considered at the genus level because of uncertain
200 identification and potential hybridization. We then used the total number of taxa and
201 their density (number of points where present divided by 75 and multiplied by 100 %),
202 pooling the three transects together for each site as dependent variables in subsequent
203 analyses, but for simplicity we will use the term species instead of taxa throughout the
204 paper. Species density may exceed a hundred percent, because of vertical overlap of
205 individuals at each sampling point.

206 2.3. *Plant species groups*

207 We first calculated the richness and density of total, native and non-native species. Non-
208 native species represent potential threats to native riparian plant communities and can
209 pose challenges to restoration measures (Richardson et al., 2007; González et al., 2018).
210 Species origin was determined based on their chorology, i.e. introduced species
211 originated from America, Africa and Asia, according to the Baseflor database (Julve,
212 1998) as well as information available from the DAISIE database ([http://www.europe-](http://www.europe-aliens.org/)
213 [aliens.org/](http://www.europe-aliens.org/)). We then considered the richness and density of hygrophilous and shade-
214 tolerant species, based on Ellenberg's indicator values (Ellenberg et al., 1992) extracted
215 from the Baseflor database (Julve, 1998). Species having indicator values for soil
216 moisture requirements ≥ 6 were considered hygrophilous; species having indicator
217 values for light requirements ≤ 6 were considered shade-tolerant (Appendix S2). These
218 classification criteria are derived from data examination and consistency between
219 moisture (F) and light (L) Ellenberg indicator values, the wetland indicator status of the
220 US National Wetland Inventory (Reed, 1988) and the light requirement classification in
221 the TOPIC database (Aubin et al., 2012). Finally, we considered the richness and
222 density of ruderal and competitive species using Grime's CSR scheme (Grime, 1977),
223 extracted from the list of CSR categorical strategies, adapted from Pierce et al. (2017).
224 Finally, species were grouped as hygrophilous, ruderal, shade-tolerant, and competitive
225 to compare succession over time among stabilization structures. In riparian zones,
226 hygrophilous species tend to occur in the lowest elevated and more frequently flooded
227 fluvial landforms, typical of early stages of the biogeomorphological succession (e.g.,
228 point bars, off-channel depressions, abandoned channels, Corenblit et al., 2009).
229 Ruderal species are well-adapted to low stress and high disturbance environments and

230 also characterize pioneer communities in the early stage of vegetation succession
231 (González et al., 2017a). Shade-tolerant species arrive later, as the overstory canopy
232 develops (McClain et al., 2011). Competitive species are well-adapted to low stress and
233 low disturbance environments and characterize post-pioneer communities in the mid- to
234 late seral successional stages (Johnson et al., 1976; Van Pelt et al., 2006).

235 *2.4. Environmental variables*

236 We collected measurements of spatial (i.e. altitude, latitude, longitude),
237 geomorphological (i.e. stream width), climatic (i.e. precipitation and temperature) and
238 land cover (i.e. proportion of forest, agriculture and urban areas in the surrounding
239 landscape) environmental variables in addition to characterizing the riverbank condition
240 (age and type of stabilization structure). Spatial and geomorphological variables were
241 measured directly on each riverbank site using a GPS and laser rangefinder. Climatic
242 variables were derived from the WorldClim climatic model (Hijmans et al., 2005) and
243 adjusted for the effect of altitude following Zimmermann and Kienast (1999). Land
244 cover variables were measured within a 500-m-radius around each riverbank site with
245 the QGIS Geographic Information System (QGIS Development Team, 2015). We
246 determined whether environmental variables varied among the three stabilization
247 structures using one-way ANOVAs for each environmental variable with Tukey's HSD
248 post hoc tests. The goal of this analysis was to verify that differences in plant
249 composition were mainly due to the experimental design (riverbank stabilization
250 structures and age) and not to environmental variables. Because we only detected a
251 significant difference in stream width between mixed sites (higher) and ripraps (lower)
252 (One-way ANOVA and Tukey HSD test, Appendix S3) and no differences in any of the
253 other environmental variables were found between the three stabilization structure

254 types, we did not use either environmental variables as a covariable in the statistical
255 analysis of vegetation (see below).

256 2.5. *Statistical analysis of vegetation*

257 To determine whether the plant species pool (gamma diversity) differed among
258 stabilization structures, we used species accumulation curves with Monte Carlo
259 randomization tests ($n = 999$), and the function `c2cv` in the *rich* package (Rossi, 2011).

260 The plant species pool was assessed considering either all species, and by groups (non-
261 native, hygrophilous, ruderal, shade-tolerant, competitive species).

262 To determine whether plant species richness and density (for all species and each
263 species group individually) varied in bioengineering stabilization structures compared to
264 ripraps or with their age, or a combination of both factors, we used Generalized Linear
265 Mixed Models (GLMM) with site proximity (see explanation below) as a random effect
266 and the functions `glmer` and `glmer.nb` in the *lme4* package (Bates et al., 2018). Site
267 proximity was a categorical variable that grouped sites within circular units of 40
268 kilometers of diameter (Appendix S1). A group of sites could encompass sites in the
269 same reach or in different streams. We chose 40 km because we estimated this distance
270 encompassed homogeneous environmental conditions, and because no sites could
271 belong to two groups using this value. This random effect made it possible to account
272 for spatial autocorrelation between close sites. We developed four *a priori* models,
273 including the random effect – Structure (riverbank stabilization structure); Age;
274 Structure + Age (additive effect of both factors); Structure*Age (additive effect and
275 multiplicative interaction); and the null model (i.e. the intercept and random effect only
276 model), and fitted Poisson GLMM for species richness and negative binomial GLMM

277 for vegetation density (total and by group). Variance explained by GLMMs was
278 estimated using the marginal coefficient of determination for fixed effect parameters
279 alone (Nakagawa et al., 2017) and the most parsimonious regression model was
280 identified using Akaike's information criterion corrected for small sample sizes (i.e.
281 AICc, Burnham and Anderson, 2002). When the delta AICc with the second best model
282 was > 2 , evaluated using the function `model.sel` in the *MuMIn* package (Barton, 2015),
283 estimated parameters and associated unconditional standard errors were extracted from
284 the top-ranked model only, and when < 2 , from the most complex of the top-ranked
285 models (Burnham and Anderson, 2002).

286 We used multivariate generalized linear models to test whether plant species
287 composition varied across stabilization structure and the age of the structure, as well as
288 the interaction between both of these factors, with *mvabund* package (Wang et al.,
289 2012). This approach makes it possible to test the effects of the predictor variables
290 (stabilization structure and age) on both community-level response and the responses of
291 individual species (Warton et al., 2015). In this case, we fitted a negative binomial
292 distribution to the abundance data for plant species that were present in more than 5 %
293 of the studied sites (i.e. 105 species). In addition to the model described above, we ran a
294 full model without the five most commonly planted species in bioengineering structures
295 (willows) to assess whether they had a disproportionate weight in the model. More
296 details on the computation of the multivariate generalized linear models (explanatory
297 data analysis, model fitting and checking) are provided in Appendix S4.

298 We also ran a canonical analysis of principal coordinates (CAP, Anderson and Willis,
299 2003) with the Bray-Curtis distance community matrix constrained by the stabilization
300 structures and their age, using the *capscale* function of the *vegan* package (Oksanen et

301 al., 2013). Ordinations such as CAP have the advantage of summarizing the main
302 gradients of multivariate variability in a few axes that can be depicted in a
303 multidimensional space (usually bidimensional, two main axes), thus providing an
304 illustrative graphical representation of overall patterns. All analyses were conducted
305 with R version 3.3.2 (R Core Team, 2017).

306

307 **3. Results**

308 *3.1. Effect of the type of stabilization structure and age on species richness and density*

309 Overall, 261 species of plants were recorded at the 42 sites for an average of 25 species
310 per site. Only a small fraction (5.7%) of these species were non-native (15 species),
311 with an average of 1.5 species per site. One third (34%) of the species were
312 hygrophilous (89 species), a similar proportion were shade-tolerant (29%, 75 species),
313 and ruderal (29%, 77 species), while one fourth (23%) were competitive (61 species).

314 The species pool was 157 species for pure structures, 178 for mixed structures and 114
315 for riprap structures (Table 1). The species pool for total, shade-tolerant and competitive
316 groups was significantly higher on mixed and pure sites, compared to ripraps. There
317 were more hygrophilous species (accumulated) in pure sites than in ripraps, more
318 ruderal in mixed sites than in ripraps, and more non-native in pure sites than in mixed
319 sites (Table 1). Even though plateaux were not reached (Appendix S5), the
320 accumulation of species slowed down with increasing number of sites and was a good
321 indicator of an appropriate sampling effort.

322 We observed differences in species richness between types of stabilization structures,
323 but some interactions with age were significant for some species groups (Table 2 and 3,

324 and Figure 3). Total species richness was higher on mixed and pure than on riprap sites
325 and remained stable with time (Figure 3a, Table 3). This pattern was also reflected in
326 ruderal species (Figure 3d, and Table 3). Hygrophilous species richness was higher on
327 pure and mixed sites, compared to ripraps, and decreased with time on the
328 bioengineered sites, but not in ripraps (Figure 3c and interaction Age:Riprap-Pure,
329 Table 3). For shade-tolerant and competitive species, species richness increased with
330 time on pure bioengineering but slightly decreased on mixed sites; richness of
331 competitive species increased with time on ripraps (Figure 3e, f and interaction
332 Age:Riprap-pure, Table 3). Richness of non-native species did not change over time
333 with any type of stabilization structure, nor did it differ between them (Figure 3b, Table
334 3).

335 Plant density also differed greatly among stabilization structures but some interactions
336 with age occurred as well (Table 2 and Figure 4). Plant density was significantly lower
337 on ripraps than on pure and mixed sites for total, ruderal and competitive species
338 (Figure 4a, d, f and Riprap-Mixed and Riprap-Pure, Table 3). Density decreased for
339 hygrophilous and increased for shade-tolerant species on pure sites, compared to ripraps
340 (Figure 4c, e and Age:Riprap-Pure, Table 3). Non-native species did not show
341 differences in density between stabilization structures and age (Figure 4b, Table 3).

342 *3.2. Effect of type of stabilization structure and age on species composition*

343 The changes in the entire plant species composition with time since completion of the
344 stabilization work differed among the three stabilization structures (interaction Structure
345 x Age: Deviance = 328.1, $p = 0.006$). However, most of the variation in species
346 composition was related to the type of stabilization structure (Deviance = 518.9, $p =$

347 0.001), rather than to the age of the structures (Deviance = 191.4, $p = 0.019$). Pairwise
348 comparisons revealed that significant differences in species composition occurred
349 between mixed and riprap sites (Deviance = 282.0, $p = 0.001$), and between pure and
350 riprap sites (Deviance = 276.7, $p = 0.001$), but not between mixed and pure sites
351 (Deviance = 158.9, $p = 0.172$). The full model run without the five species most
352 commonly planted in bioengineering structures (willows) showed a similar relative
353 contribution of type of stabilization structure and age (Structure: Deviance = 439.3, $p =$
354 0.01 ; Age: Deviance = 170.9, $p = 0.04$), compared to the models run with the five
355 species, but a decrease of the total deviance of the model (Total deviance = 1649.8,
356 models not shown), compared to the model including the five planted species (Total
357 deviance = 1814.5).

358 The effect of the stabilization structure on plant composition is well illustrated by the
359 first axis of the canonical analysis of principal coordinates (Figure 5), which clearly
360 separated ripraps (negative end of Axis 1) from bioengineering sites (positive end of
361 Axis 1), while the second axis showed only a slight relationship to the age of the
362 stabilization structure (older sites more positively loaded, Axis 2). Plant communities
363 from ripraps were more clustered (shorter grey lines, Figure 5) than those from pure and
364 mixed sites (longer grey lines, Figure 5), indicating a greater similarity in species
365 composition along the chronosequence for this stabilization structure. Despite the
366 relatively low percentage of variability explained by the ordination ($R^2_{adj} = 10.3\%$, $p =$
367 0.001), the individual terms of the CAP model were highly significant (Age: $p = 0.021$;
368 Structure: $p = 0.001$).

369 Univariate tests (Appendix S7) revealed that few species contributed to the multivariate
370 significant effect, i.e. the variation in the abundance of these species captured a large

371 amount of the deviance explained by the model. *Cornus sanguinea* (Deviance = 23.5,
372 $p_{adj} = 0.027$), *Lonicera xylosteum* (Deviance = 23.1, $p_{adj} = 0.028$), *Crataegus monogyna*
373 (Deviance = 18.4, $p_{adj} = 0.064$), *Salix purpurea* (Deviance = 16.9, $p_{adj} = 0.096$), *Salix*
374 *alba* (Deviance = 15.5, $p_{adj} = 0.158$) and *Salix triandra* (Deviance = 12.7, $p_{adj} = 0.318$)
375 were more closely related to mixed/pure structures than to ripraps. The ligneous species
376 *Corylus avellana* and *Cornus sanguinea* were highly associated to old mixed/pure
377 structures (Deviance = 20.4, $p_{adj} = 0.033$; Deviance = 6.083, $p_{adj} = 0.989$, respectively,
378 Appendix S7), while *Vicia sativa* (Deviance = 12.4, $p_{adj} = 0.106$) was more closely
379 related to young structures (i.e. < 5 years).

380 **4. Discussion**

381 Our results show that plant composition and its trajectory over time differed between
382 soil bioengineering and civil engineering structures. Pure and mixed stabilization
383 structures had higher richness and density of plant species than ripraps, and comprised
384 different species assemblages. Moreover, we found that the successional trajectories of
385 riparian communities differed among the three types of stabilization structures, with
386 more stagnant vegetation on ripraps than on the two other types of sites. As we
387 predicted, these findings show that soil bioengineering not only plays a role in erosion
388 control and riverbank stabilization, but also fosters plant diversity by promoting
389 vegetation succession following the active introduction of pioneer ligneous species.

390 *4.1. Bioengineering and ripraps lead to different plant species diversity and* 391 *composition*

392 Our findings supported those of previous studies (Cavaillé et al., 2013; Schmitt et al.,
393 2018), determining that soil bioengineering techniques enhanced the richness and

394 density of riparian vegetation better than ripraps. Indeed, except for non-native species,
395 total species pool (cumulative) and mean species richness (locally by site) of all species
396 groups were greater on riverbanks stabilized by either pure or mixed structures than on
397 riverbanks entirely stabilized by ripraps. This pattern was especially marked for shade-
398 tolerant and competitive species on pure structures. Differences in environmental
399 conditions (light, soil moisture) and in biotic interactions between the pure (and to a
400 lesser extent the mixed) and riprap techniques may explain the pattern. By forming
401 dense thickets on bioengineered sites, *Salix viminalis*, *S. purpurea* and *S. triandra* may
402 decrease flow speed and enhance fine sediment retention (Rey and Burylo, 2014) on the
403 lower part of the riverbank, which in turn should increase seed retention of
404 hydrochorous species and ultimately favour riparian plant diversity (Corenblit et al.,
405 2016; Mikuś et al., 2013). Also, by modifying local conditions (e.g., reducing light
406 availability and shear stress), the active introduction of ligneous species may favour
407 shade-tolerant and competitive riparian plant species (González et al., 2017a; Lennox et
408 al., 2011), particularly in pure structures where ligneous species are planted across the
409 entire surface, from the bottom to the top of the bank. Our results thus concur with the
410 “Field of Dreams Hypothesis” (Palmer et al., 1997), which assumes that a more
411 complex vegetation structure established by revegetation efforts will allow other plants
412 to recolonize a restored habitat.

413 Although we found clear evidence that bioengineering structures favor plant diversity
414 better than ripraps, the findings of our study differ slightly from those reported
415 previously, which showed higher richness on mixed structures compared to pure
416 structures for plants and other trophic groups (Cavaillé et al., 2013). Mixed structures
417 provide a greater heterogeneity of environmental conditions, with inert materials

418 (riprap) on the lower part of the bank and willow cuttings and plantings on the upper
419 part. Such a combination of techniques will increase species richness only if distinct
420 flora establishes on the riprap area compared to the upper planted part of the riverbank.
421 In our study, ripraps were shown to be inhospitable to most plants, being less densely
422 colonized in general; therefore, they contributed little to increasing the plant richness of
423 mixed sites. This hypothesis of poor colonization of ripraps in our study sites was even
424 confirmed for non-native species, which are normally able to colonize such structures
425 but were mostly absent from ours. For example, civil engineering structures along
426 waterways have been identified as habitats that promote non-native invasive species
427 such as *Fallopia japonica* (Francis and Hoggart, 2009). Even though we found no
428 statistical evidence that riprap sites were colonized more by non-native species than
429 mixed and pure bioengineered sites, examination of the constrained ordination plot
430 revealed a close association between the occurrence of *Fallopia japonica* and entirely
431 riprapped riverbanks. Indeed, the mean density of this highly invasive species was twice
432 as high on ripraps (mean \pm SD = 10.3 ± 25.5) as on bioengineering structures (pure =
433 5.4 ± 14.5 ; mixed = 2.6 ± 6.7). Dommanget et al. (2019) reported a poorer performance
434 by *F. japonica* under a dense canopy cover of *Salix* species in mesocosm experiments,
435 which suggests that bioengineering could also help limit the propagation of invasive
436 species, more so than ripraps.

437 4.2. Successional trajectories also differ in bioengineered and riprap sites

438 Much as the type of stabilization structure influenced diversity patterns, time post-
439 stabilization was a powerful predictor of plant species richness and density. The
440 occurrence of certain groups of species based on their ecological requirements, i.e. soil
441 moisture and light, as well as competitive strategies, changed along the chronosequence.

442 Specifically, the richness of hygrophilous species decreased over time, notably in the
443 case of bioengineering structures, possibly due to fine sediment aggradation along
444 stabilized riverbanks (Corenblit et al., 2009) or to a shift in trade-offs from hygrophilous
445 to shade-tolerant species in older sites dominated by dense willow stands (Gurnell et al.,
446 2012). However, repeated observations on the same sites would have been necessary to
447 confirm this hypothesis. Changes in environmental conditions that accompany
448 aggradation and hydrological disconnection typical of biogeomorphological succession
449 theoretically favor colonization by species with different resource acquisition strategies
450 (Corenblit et al., 2009; Tabbachi et al., 2019). Nitrogen-demanding species more
451 adapted to drought stress and shade conditions (e.g. *Alnus glutinosa*, *Corylus avellana*,
452 *Crataegus monogyna*, *Equisetum arvense*) replaced hygrophilous species along
453 succession (Januschke et al., 2014). Our results also showed that shade-tolerant and
454 competitive species responded differently to time post-stabilization, depending on
455 whether they were on pure, mixed or riprap sites. While richness of shade-tolerant and
456 competitive species more than doubled in 14 years on pure sites, they tended to decrease
457 or remain stable on mixed and riprap sites. Overall, we believe that the decrease in
458 hygrophilous species and the increase in shade-tolerant and competitive species over
459 time is related to similar successional trajectories observed in riparian forests that
460 follow a linear succession, i.e. a shift from pioneer phreatophyte species to post pioneer
461 drought-adapted species along succession (e.g. Fierke and Kauffman, 2005; Muñoz-
462 Mas et al., 2017; Van Pelt et al., 2006). Thus, in accordance with previous studies, our
463 results support the idea that planting ligneous species in riparian zones can foster
464 succession (McClain et al., 2011; Osman and Barakbah, 2011) and favor biodiversity
465 (Lennox et al., 2011), making soil bioengineering a good compromise solution for the

466 restoration of eroding riverbanks. Conversely, ripraps did not show evidence of
467 succession and remained less densely colonized by only a few species, including light
468 tolerant and xerophytic species such as *Fallopia japonica*, *Festuca rubra*, *Robinia*
469 *pseudoacacia*, and *Sanguisorba officinalis* (see mean densities in Appendix S7).
470 Ripraps thus remained “blocked” in the early stages of vegetation succession,
471 dominated by pioneer light-demanding and not strictly riparian vegetation (Wollny et
472 al., 2019). The fact that the plant community composition in ripraps was rather simple
473 could also explain their higher similarity as a group (as shown on the CAP ordination),
474 compared to the more heterogeneous communities in the other two types of stabilization
475 structures.

476

477 **5. Conclusion**

478 Overall, our results illustrated the ecological added-value of soil bioengineering
479 techniques, through the active introduction of native shrubs to support riparian plant
480 species. Previous research highlighted the role of native shrubs as the ecological
481 engineers of river ecosystems. Here, soil bioengineering with *Salix* spp. promoted
482 vegetation succession on stabilized riverbanks, through the recruitment and
483 establishment of specific plant species groups, mainly shade-tolerant and competitive
484 ones. As a result, soil bioengineering increased riparian plant richness and density,
485 reinforcing the idea that this nature-based solution is a good compromise between
486 erosion control with civil engineering structures and other forms of ecological
487 restoration that cannot be applied in this context. Even though bioengineering can also

488 be designed to resist high shear stress, these techniques should be applied wherever
489 erosion constraints are low and hard civil engineering may be unnecessary.

490 Conversely, community composition of ripraps did not change over time and remained
491 species-poor, suggesting that civil engineering techniques should only be used in
492 specific contexts where bioengineering techniques cannot be implemented, such as on
493 sites dominated by clay, which represent high constraints for root development, or
494 where scouring conditions are incompatible with the best available bioengineering
495 techniques. Nonetheless, the plant diversity dynamics in ripraps need to be studied for
496 longer periods of time to verify if our findings hold true.

497 Many questions remain, most importantly, those regarding the contribution of soil
498 bioengineering to regional diversity and factors associated with patterns at the landscape
499 scale. Comparing our results with the regional species pool, for example, would help to
500 quantify the role of stabilization structures in regional biodiversity protection. It is also
501 important to note that succession, particularly in riparian systems, is not always a
502 deterministic linear process, and bifurcations, multiple pathways and regressions are
503 common. It should also be kept in mind that bank erosion is a natural process that
504 promotes dynamic habitats crucial for aquatic and terrestrial biodiversity in stream
505 ecosystems, and in that sense, restoration of entire river segments that embraces channel
506 migration may be preferable over undertaking stabilization work in contexts where
507 public safety is not at risk. Considering natural or near-natural riparian zones as
508 desirable reference endpoints for stabilization structures would be helpful to consider all
509 these aspects in future studies.

510

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522

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765 Zimmermann, N. E., Kienast, F., 1999. Predictive mapping of alpine grasslands in
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768 **Tables**

769 Table 1. Variations in the pool (cumulative number of species in all sites) and the mean (\pm SD) of riparian plant species richness in relation to the
 770 type of stabilization structure. Letters indicate homogeneous groups of stabilization structure types after Monte Carlo randomization tests (n =
 771 999).

Variable	Total (n = 42)		Type of stabilization structure					
	Pool	Mean (\pm SD)	Pure (n = 15)		Mixed (n = 13)		Riprap (n = 14)	
			Pool	Mean (\pm SD)	Pool	Mean (\pm SD)	Pool	Mean (\pm SD)
Total	261	24.93 (\pm 9.45)	157 a	25.93 (\pm 7.88)	178 a	32.38 (\pm 8.09)	114 b	16.93 (\pm 5.37)
Non-native	15	1.50 (\pm 1.13)	13 a	1.80 (\pm 1.21)	6 b	1.46 (\pm 1.33)	9 ab	1.21 (\pm 0.80)
Hygrophilous	89	8.64 (\pm 4.52)	61 a	10.47 (\pm 4.50)	53 ab	9.46 (\pm 4.12)	43 b	5.93 (\pm 3.81)
Ruderal	77	6.95 (\pm 3.70)	43 ab	7.00 (\pm 4.02)	53 a	8.92 (\pm 3.73)	37 b	5.07 (\pm 2.27)
Shade-tolerant	75	7.29 (\pm 4.06)	50 a	7.67 (\pm 4.40)	51 a	10.38 (\pm 2.81)	23 b	4.00 (\pm 1.57)
Competitive	61	6.93 (\pm 2.89)	44 a	6.93 (\pm 2.96)	45 a	9.00 (\pm 2.42)	27 b	5.00 (\pm 1.80)

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774 Table 2. Top-ranking models predicting richness and density of total, non-native,
775 hygrophilous, ruderal, shade-tolerant, and competitive plant species in relation to stabilization
776 structure age and type in the foothills of the Alps and Jura Mountains (France and
777 Switzerland), as assessed with Akaike's information criterion corrected for small sample size
778 (AICc). The number of parameters estimated, including the intercept and random effect (k),
779 AICc, AICc weight (W) and marginal coefficient of determination for fixed effects (R²), are
780 provided (details on all *a priori* models are reported in Appendix S6). "Structure" refers to the
781 riverbank stabilization types.

Variable	Species group	Top-ranked model	k	AICc	W	R ² _{GLMM}
Richness	Total	Structure	4	294.5	0.498	0.568
	Non-native	Null	2	127.5	0.571	0.000
	Hygrophilous	Structure + Age	5	247.2	0.648	0.352
	Ruderal	Structure	4	224.8	0.647	0.271
	Shade-tolerant	Structure*Age	7	219.3	0.810	0.597
	Competitive	Structure + Age	5	199.9	0.420	0.320
Density	Total	Structure	5	484.1	0.673	0.645
	Non-native	Null	3	289.0	0.694	0.000
	Hygrophilous	Structure	5	462.0	0.448	0.366
	Ruderal	Structure	5	405.5	0.725	0.323
	Shade-tolerant	Structure*Age	8	397.0	0.588	0.574
	Competitive	Structure	5	404.8	0.524	0.156

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785 Table 3. Estimated coefficients (Estimate (\pm SE)) and confidence intervals (95% CI) for each variable used to predict the richness and density of
786 total, non-native, hygrophilous, ruderal, shade-tolerant, and competitive plant species in relation to stabilization structure type and age in the
787 foothills of the Alps and the Jura Mountains (France and Switzerland). The 95% confidence interval of coefficients in bold excluded 0 ("-"
788 indicates no possible estimate and associated standard errors). More details on all *a priori* models developed and their parameters are given in
789 Appendix S6.

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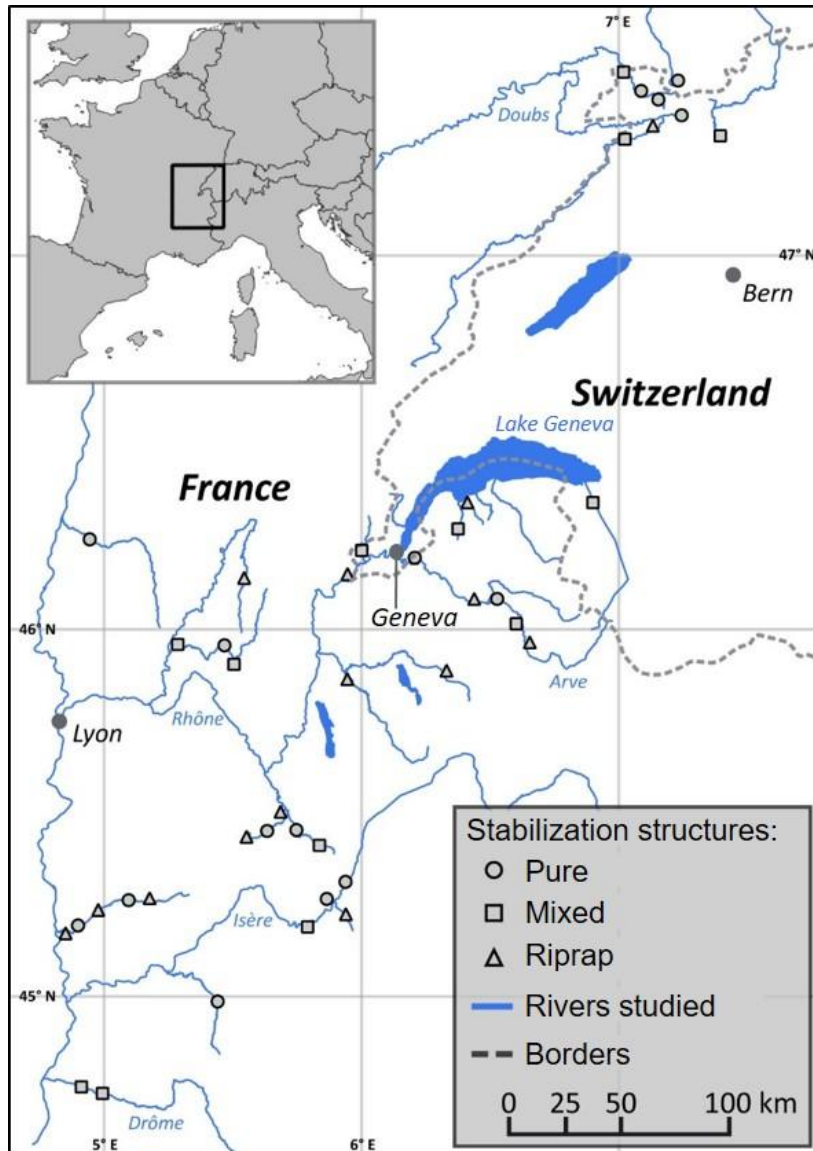
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Variable	Species group	Riprap-Mixed		Riprap-Pure		Age	
		Estimate (\pm SE)	(95% CI)	Estimate (\pm SE)	(95% CI)	Estimate (\pm SE)	(95% CI)
Richness	Total	0.624 (\pm 0.090)	(0.448; 0.800)	0.421 (\pm 0.088)	(0.249; 0.593)	-0.014 (\pm 0.010)	(-0.034; 0.006)
	Non-native	-	-	-	-	-	-
	Hygrophilous	0.413 (\pm 0.154)	(0.111; 0.715)	0.517 (\pm 0.144)	(0.235; 0.799)	-0.042 (\pm 0.017)	(-0.075; -0.009)
	Ruderal	0.549 (\pm 0.156)	(0.243; 0.855)	0.308 (\pm 0.156)	(0.002; 0.614)	-0.017 (\pm 0.016)	(-0.048; 0.014)
	Shade-tolerant	0.764 (\pm 0.289)	(0.198; 1.330)	-0.144 (\pm 0.313)	(-0.757; 0.469)	-0.049 (\pm 0.034)	(-0.116; 0.018)
	Competitive	0.776 (\pm 0.292)	(0.204; 1.348)	0.029 (\pm 0.314)	(-0.586; 0.644)	0.022 (\pm 0.028)	(-0.033; 0.077)
Density	Total	0.968 (\pm 0.134)	(0.705; 1.231)	1.012 (\pm 0.124)	(0.769; 1.255)	-	-
	Non-native	-	-	-	-	-	-
	Hygrophilous	1.621 (\pm 0.609)	(0.427; 2.815)	2.513 (\pm 0.589)	(1.359; 3.667)	0.026 (\pm 0.055)	(-0.082; 0.134)
	Ruderal	1.078 (\pm 0.267)	(0.555; 1.601)	0.977 (\pm 0.261)	(0.465; 1.489)	0.021 (\pm 0.027)	(-0.032; 0.074)
	Shade-tolerant	0.815 (\pm 0.469)	(-0.104; 1.734)	0.001 (\pm 0.469)	(-0.918; 0.920)	-0.095 (\pm 0.044)	(-0.181; -0.009)
	Competitive	0.496 (\pm 0.261)	(-0.016; 1.008)	0.671 (\pm 0.252)	(0.177; 1.165)	-	-

Variable	Species group	Age:Riprap-Mixed		Age:Riprap-Pure	
		Estimate (\pm SE)	(95% CI)	Estimate (\pm SE)	(95% CI)
Richness	Total	-	-	-	-
	Non-native	-	-	-	-
	Hygrophilous	-	-	-	-
	Ruderal	-	-	-	-
	Shade-tolerant	0.029 (\pm 0.041)	(-0.051; 0.109)	0.122 (\pm0.042)	(0.040; 0.204)
	Competitive	-0.028 (\pm 0.037)	(-0.101; 0.045)	0.047 (\pm 0.039)	(-0.029; 0.123)
Density	Total	-	-	-	-
	Non-native	-	-	-	-
	Hygrophilous	-0.070 (\pm 0.080)	(-0.227; 0.087)	-0.185 (\pm0.077)	(-0.336; -0.034)
	Ruderal	-	-	-	-
	Shade-tolerant	0.100 (\pm 0.062)	(-0.022; 0.222)	0.209 (\pm0.063)	(0.086; 0.332)
	Competitive	-	-	-	-

806 **Figure captions**

807 Figure 1. Study sites with riverbank protection structures in the foothills of the Alps and the
808 Jura Mountains (France and Switzerland).



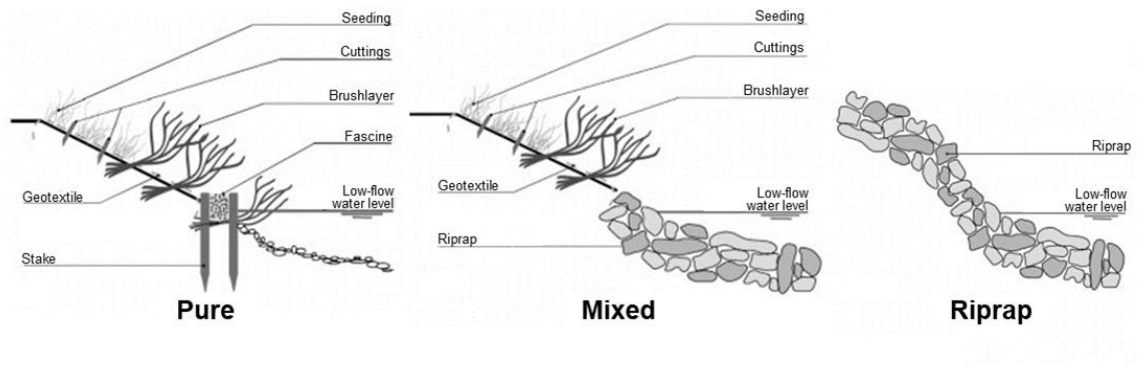
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813 Figure 2. Schematic drawing of the three types of riverbank stabilization structures: "Pure"
814 bioengineering technique, with plant material only, "Mixed" technique combining civil and
815 bioengineering techniques, "Riprap" protection, with mineral material only. Adapted from
816 Figure 1, Cavaillé et al., 2013.

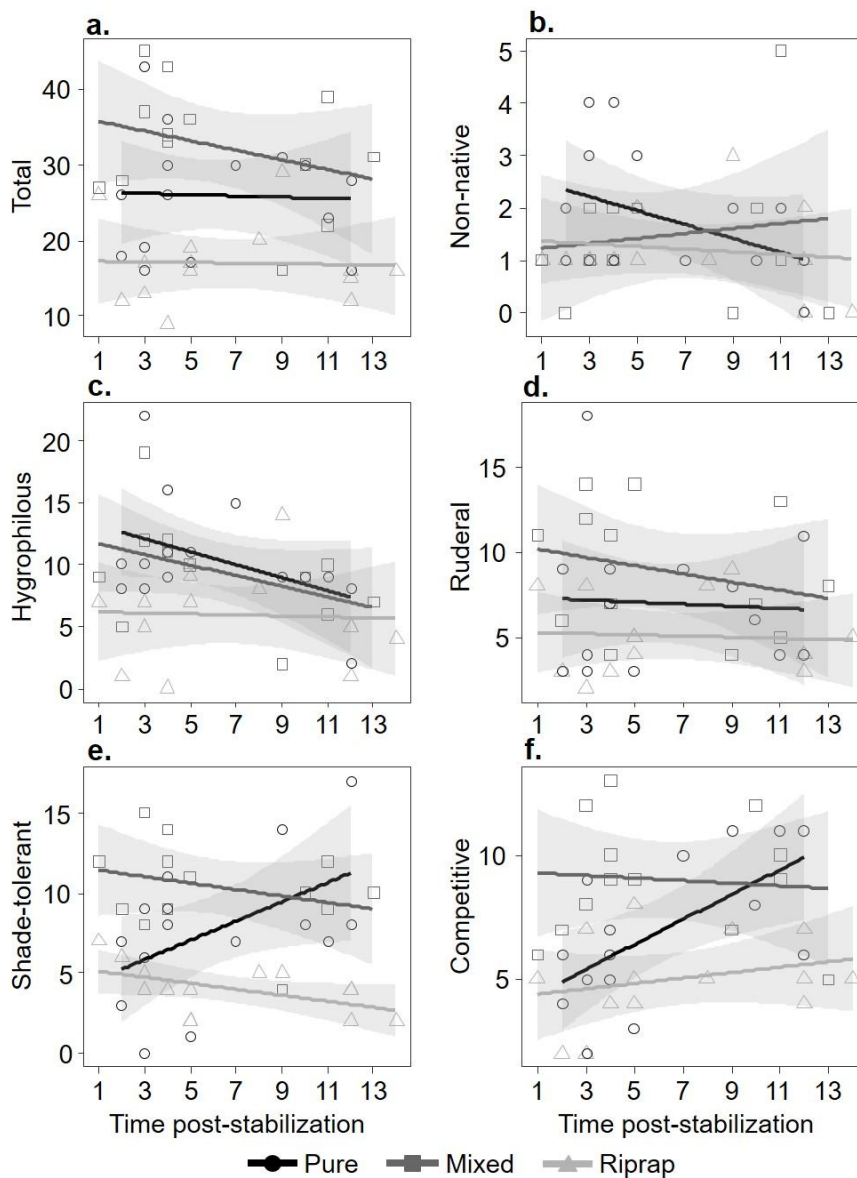


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820 Figure 3. Variation in species richness (i.e., number of species) of (a) total, (b) non-native, (c)
 821 hygrophilous, (d) ruderal, (e) shade-tolerant, and (f) competitive plant species in relation to
 822 stabilization structure age and among pure (n = 15) and mixed (n = 13) bioengineering and
 823 riprap (n = 14) stabilization structures in the foothills of the Alps and the Jura Mountains
 824 (France and Switzerland).



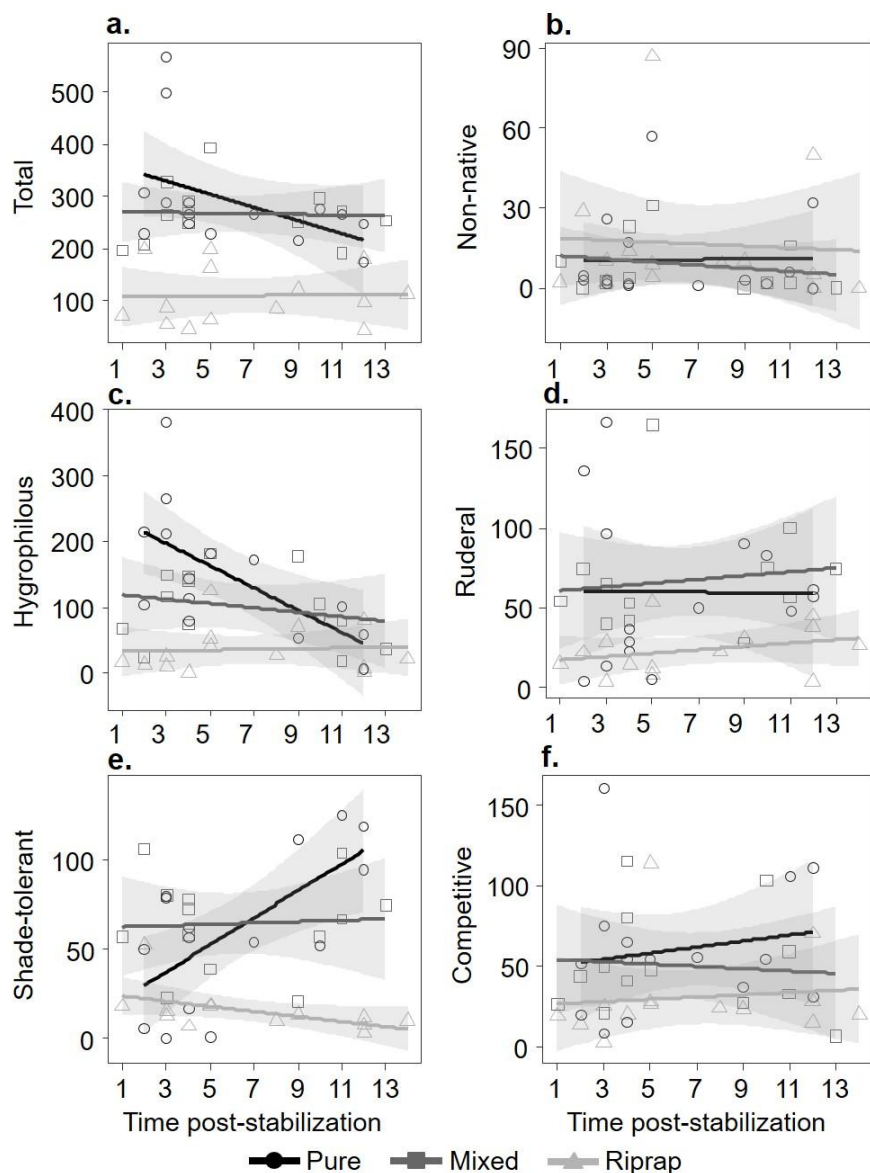
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828 Figure 4. Variation in species density (frequency of occurrence with vertical overlap) of (a)
 829 total, (b) non-native, (c) hygrophilous, (d) ruderal, (e) shade-tolerant, and (f) competitive plant
 830 species in relation to stabilization structure age and among pure (n = 15) and mixed (n = 13)
 831 bioengineering and riprap (n = 14) stabilization structures in the foothills of the Alps and the
 832 Jura Mountains (France and Switzerland).

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835 Figure 5. Biplot of the first two axes of a canonical analysis of principal coordinates (CAP) of
 836 plant species composition in the foothills of the Alps and the Jura Mountains (France and
 837 Switzerland). Only the scores of the most determinant species (higher deviance) and the
 838 scores of sites are displayed. Symbols of site scores represent the three different stabilization
 839 structure types. The size of the symbols is proportional to the time since completion of the
 840 stabilization work. Native species are shown in blue, non-native in red (the complete list of
 841 species with univariate tests for age, structure and their interaction is reported in Appendix
 842 S7). Contribution of the constrained model (R^2 adjusted) and CAP axes 1 and 2 to the
 843 variation of community composition is provided in the upper right corner and the two axes,
 844 respectively. The grey lines connect each site to the centroid of the corresponding riverbank
 845 stabilization type.

