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

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Highlights

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

Abstract

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

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

Keywords

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

1. Introduction

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

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

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

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

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

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

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

2. Material and methods

2.1. Study area and sampling design

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

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

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

2.2. Vegetation survey

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

2.3. Plant species groups

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

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

2.4. Environmental variables

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

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

2.5. Statistical analysis of vegetation

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

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

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

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

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

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

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

3. Results

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

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

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

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

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

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

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

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

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

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

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

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

4. Discussion

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

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

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

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

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

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

4.2. Successional trajectories also differ in bioengineered and riprap sites

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

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

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

5. Conclusion

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

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

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

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

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 766 Switzerland: species versus community approach. *Journal of Vegetation Science* 10,
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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					
			Pure (n = 15)		Mixed (n = 13)		Riprap (n = 14)	
	Pool	Mean (\pm SD)	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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Table 2. Top-ranking models predicting richness and density of total, non-native, hygrophilous, ruderal, shade-tolerant, and competitive plant species in relation to stabilization structure age and type in the foothills of the Alps and Jura Mountains (France and Switzerland), as assessed with Akaike's information criterion corrected for small sample size (AICc). The number of parameters estimated, including the intercept and random effect (k), AICc, AICc weight (W) and marginal coefficient of determination for fixed effects (R^2), are provided (details on all *a priori* models are reported in Appendix S6). "Structure" refers to the 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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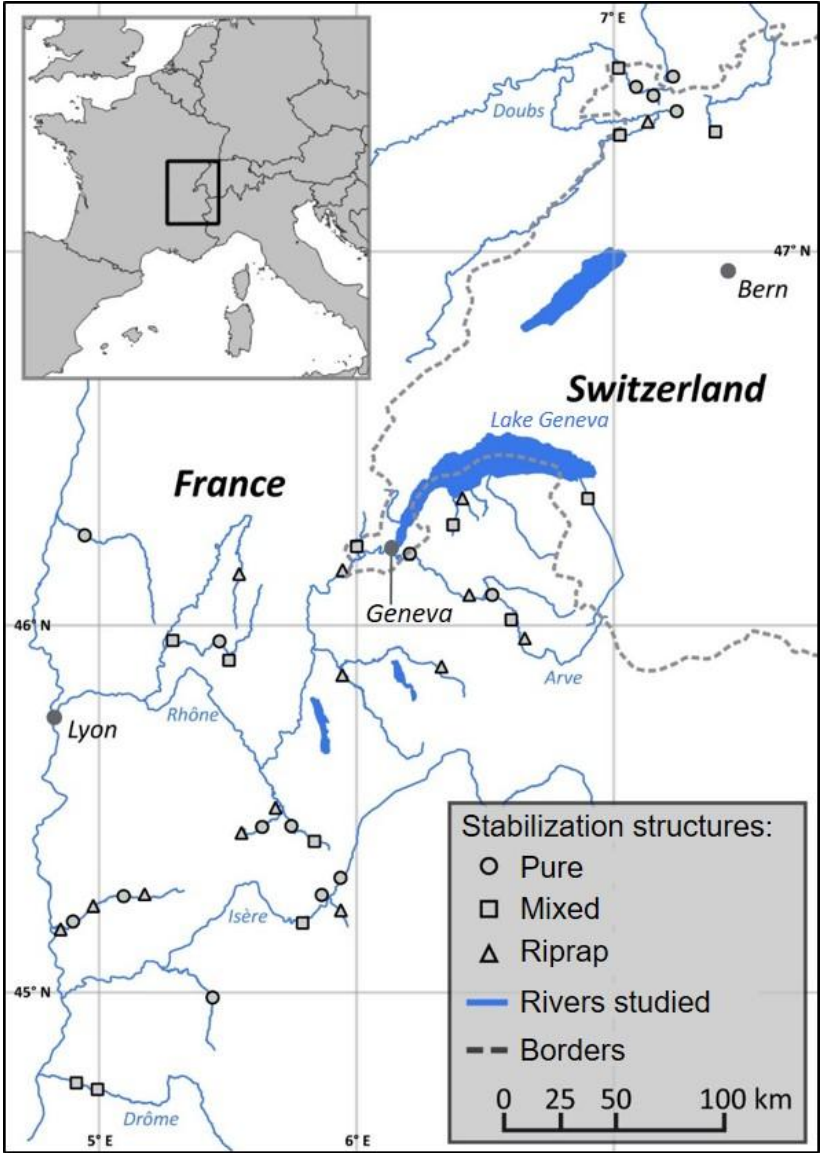
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Variable	Species group	Riprap-Mixed		Riprap-Pure		Age	
		Estimate (\pm SE)	(95% CI)	Estimate (\pm SE)	(95% CI)	Estimate (\pm SE)	(95% CI)
Richness	Total	0.624 (\pm0.090)	(0.448; 0.800)	0.421 (\pm0.088)	(0.249; 0.593)	-0.014 (\pm 0.010)	(-0.034; 0.006)
	Non-native	-	-	-	-	-	-
	Hygrophilous	0.413 (\pm0.154)	(0.111; 0.715)	0.517 (\pm0.144)	(0.235; 0.799)	-0.042 (\pm0.017)	(-0.075; -0.009)
	Ruderal	0.549 (\pm0.156)	(0.243; 0.855)	0.308 (\pm0.156)	(0.002; 0.614)	-0.017 (\pm 0.016)	(-0.048; 0.014)
	Shade-tolerant	0.764 (\pm0.289)	(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 (\pm0.292)	(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 (\pm0.134)	(0.705; 1.231)	1.012 (\pm0.124)	(0.769; 1.255)	-	-
	Non-native	-	-	-	-	-	-
	Hygrophilous	1.621 (\pm0.609)	(0.427; 2.815)	2.513 (\pm0.589)	(1.359; 3.667)	0.026 (\pm 0.055)	(-0.082; 0.134)
	Ruderal	1.078 (\pm0.267)	(0.555; 1.601)	0.977 (\pm0.261)	(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 (\pm0.044)	(-0.181; -0.009)
	Competitive	0.496 (\pm 0.261)	(-0.016; 1.008)	0.671 (\pm0.252)	(0.177; 1.165)	-	-

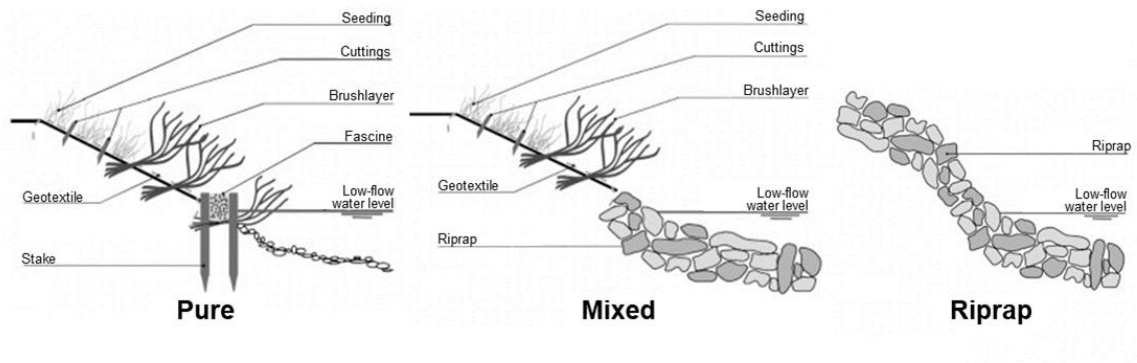
Variable	Species group	Age:Riprap-Mixed		Age:Riprap-Pure	
		Estimate (\pm SE)	(95% CI)	Estimate (\pm SE)	(95% CI)
Richness	Total	-	-	-	-
	Non-native	-	-	-	-
	Hygrophilous	-	-	-	-
	Ruderal	-	-	-	-
	Shade-tolerant	0.029 (\pm 0.041)	(-0.051; 0.109)	0.122 (\pm0.042)	(0.040; 0.204)
	Competitive	-0.028 (\pm 0.037)	(-0.101; 0.045)	0.047 (\pm 0.039)	(-0.029; 0.123)
	Total	-	-	-	-
Density	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	-	-	-	-

Figure captions

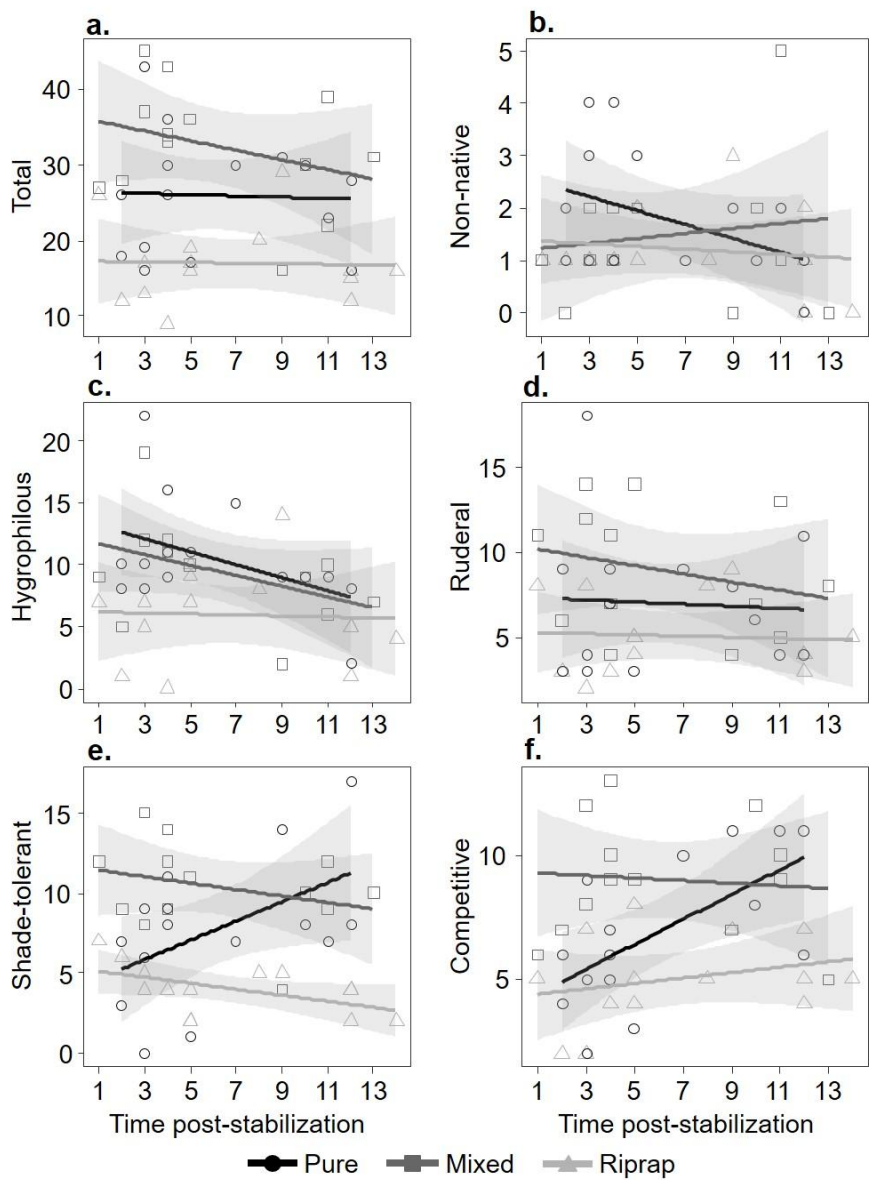
Figure 1. Study sites with riverbank protection structures in the foothills of the Alps and the Jura Mountains (France and Switzerland).



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.

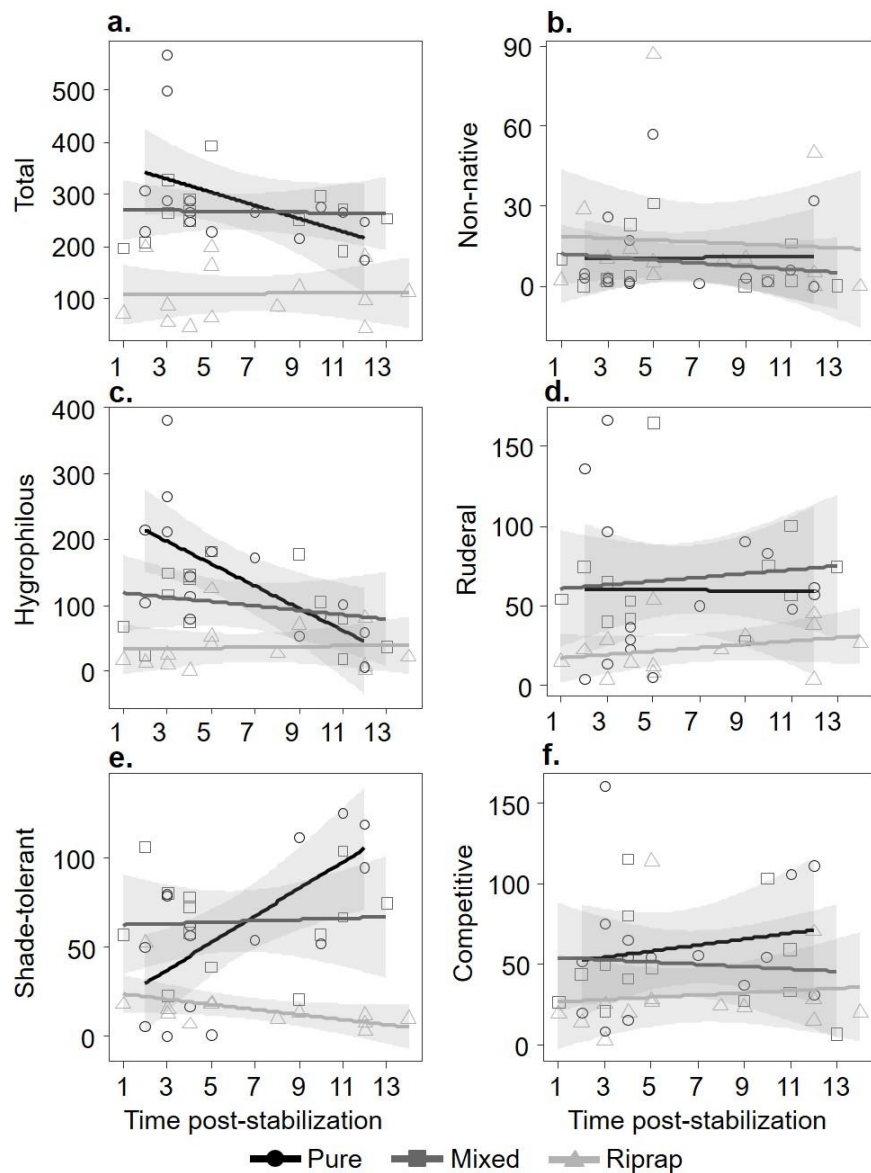


820 Figure 3. Variation in species richness (i.e., number of species) of (a) total, (b) non-native, (c)
 821 hygrophilous, (d) ruderal, (e) shade-tolerant, and (f) competitive plant species in relation to
 822 stabilization structure age and among pure (n = 15) and mixed (n = 13) bioengineering and
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

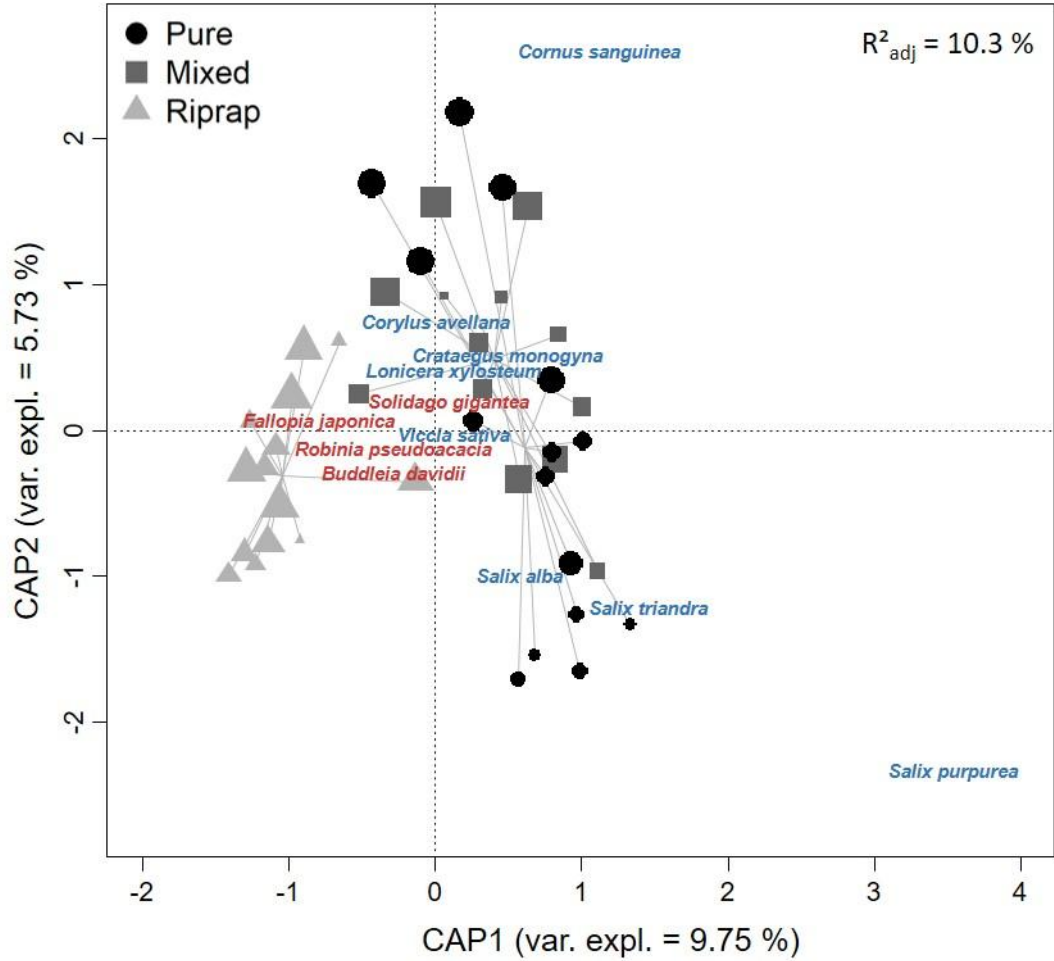


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Figure 4. Variation in species density (frequency of occurrence with vertical overlap) of (a) total, (b) non-native, (c) hygrophilous, (d) ruderal, (e) shade-tolerant, and (f) competitive plant species in relation to stabilization structure age and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



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.



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