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Soil bioengineering techniques enhance riparian habitat quality and multi-taxonomic diversity in the foothills of the Alps and Jura Mountains

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Abstract

Riparian zones have disproportional ecological importance relative to their size. For decades, the functionality of riparian zones has been altered, with detrimental consequences on biodiversity. Recently, riparian zone restoration has become a major issue. When channel mobility cannot be restored and when erosion control is of primary concern, soil bioengineering techniques are often viewed as a compromise solution. We studied 37 riverbanks, from civil engineering to soil bioengineering, plus natural willow stands, in the foothills of the Alps and Jura Mountains. Using a principal component analysis, we first studied whether terrestrial and aquatic habitat variables varied among riverbank stabilization structures and bank stabilization age and built a synthetic index of riparian habitat quality reflecting the multivariate similarity of riverbank sites. Then, using a modelling approach, we tested whether multi-taxonomic diversity responded to changes in habitat quality and to broad-scale environmental variables (i.e., climate, hydrology and land cover). Soil bioengineering techniques, especially willow fascines and to lower extend vegetated crib wall, enhanced riparian habitat quality by allowing for a greater richness and density of pioneer tree species but also for a larger cover of high quality aquatic micro-habitats. This increase in riparian habitat quality induced an increase in both terrestrial and aquatic species diversity, highlighting the added-value of soil bioengineering techniques to restore riparian biodiversity. This may confirm that stabilization structures made of willow fascines are better suited than stabilization structures made of artificial substrata to support riparian species. Also, beyond the positive effect of soil bioengineering techniques for riparian biodiversity, we found that climatic, hydrological and land cover variables strongly influenced diversity patterns. Thus, multi-taxonomic diversity decreased along larger rivers and in landscapes dominated by urban areas. This may indicate that the full added value of soil bioengineering techniques for biodiversity will only become apparent if more attention is paid to mitigating the negative

impact of human activities in the vicinity of riparian zones and if larger scale environmental parameters are taken into account as early as possible in restoration project. Therefore, we strongly recommend that riverbank restoration projects, based on the active introduction of native pioneer tree species, should be planned at the catchment scale.

Keywords: biodiversity patterns, riparian habitat quality, soil bioengineering techniques, ecological restoration, riverbank stabilization

1. Introduction

Riparian zones, i.e., ecosystems at the interface between terrestrial and freshwater habitats, are small natural features with disproportional ecological importance relative to their size (González et al., 2017). Indeed, though riparian zones represent only 1 % of the European continental area (Weissteiner et al., 2016), they host a unique species pool and are of critical concern for biodiversity conservation (Naiman and Decamps, 1997; Sabo et al., 2005). Moreover, riparian zones insure a wide range of functions (e.g., water regulation, soil retention) which directly improve human well-being by providing many ecosystem services (e.g., flood control, water quality) (Naiman and Decamps, 1997). In this context, restoring or conserving the ecological integrity of riparian zones is of great importance (Strayer and Dudgeon, 2010).

Worldwide, riparian zones have been severly impacted by human activities (Feld et al., 2011; Nilsson et al., 2005). Civil engineering has been widely used to control floods and prevent channel migration. These practices have profoundly altered the dynamics of rivers by modifying flow and sediment regimes, and consequently, have seriously impacted both aquatic and terrestrial biodiversity (Dudgeon et al., 2006; Poff et al., 2007). Moreover, the radical changes in the structure and composition of riparian vegetation (Naiman and Decamps, 1997) have favored the establishment of alien species (Pyšek et al., 2010), leading to an oversimplification of riparian biodiversity (Richardson et al., 2007).

In recent years, riparian zone restoration has become a major issue in European countries (Gumiero et al., 2013), and is being carried out both to improve biodiversity conservation and water quality. Although the removal of flood prevention infrastructures is often the most effective solution, in many cases, this is far from feasible (González et al., 2017). When channel mobility cannot be restored and when erosion control is of primary concern, soil bioengineering techniques can be viewed as an alternative solution. Soil bioengineering consists of copying naturally functioning riverbank models by using the physical proprieties of living plants, i.e., root systems provide underground soil reinforcement while foliage and stems provide surface protection from scouring (Li and Eddleman, 2002). These techniques have long been used in Europe (Evette et al., 2009) and are still common in restoration projects nowadays (González et al., 2015).

Beyond riverbank stabilization, soil bioengineering techniques are expected to have positive impacts on riparian ecosystems, by increasing the quality of wildlife habitats and water resources (Li and Eddleman, 2002). Through facilitation and amelioration processes, the active introduction of plant species may improve growing conditions for other plant species and increase local heterogeneity (Gurnell, 2014; Gurnell et al., 2012). This, in turn, is likely to benefit riparian biodiversity as a whole. Indeed, soil bioengineering techniques assume that the use of early successional species can accelerate desirable successional trajectories by forming a base structure for the desired ecosystem (Clements, 1916; Connell and Slatyer, 1977). Thus, soil bioengineering techniques are often viewed as a way to restore riparian ecosystem by favoring the establishment of native species (e.g., Holl and Crone, 2004; McClain et al., 2011) and more generally as a way to improve ecological conditions for riparian biodiversity on degraded riverbanks (e.g., Cavaillé et al., 2013; Li et al., 2006; Sudduth and Meyer, 2006; Wu and Feng, 2006).

We aimed to study the effect of soil bioengineering techniques on terrestrial and aquatic habitat quality and taxonomic diversity in the French and Swiss foothills of the Alps and Jura Mountains. We considered four different riverbank stabilization structures – riprap protection, mixed protection, vegetated crib wall and willow fascines – of different ages (i.e. occurring between 3 and 9 years prior to the study), plus natural riparian willow stands as a reference. Beyond the direct influence of riverbank protection techniques on biodiversity, we were interested in understanding whether riverbank protection techniques and bank stabilization age induced changes in riparian habitat quality and whether related changes influence multi-taxonomic diversity. Indeed, for all types of stabilization structures, vegetation cover is expected to increase over time (Bariteau et al., 2013), which may increase the magnitude of physical interactions with flows and sediments (Corenblit et al., 2007), thus enhancing habitat heterogeneity (Naiman et al., 2005). As a rule of thumb, an increase in habitat quality over time is often observed in restoration projects (e.g., Hasselquist et al., 2015; Lennox et al., 2011). To investigate the added value of soil bioengineering techniques for riparian biodiversity, it is thus critical to, first, better define sound techniques that reconcile erosion control and ecological restoration (Rey et al., 2019), second, move beyond categories of individual riverbank stabilization structure by accounting for the effects of bank stabilization age.

Specifically, we tested how selected terrestrial and aquatic habitat variables varied among riverbank stabilization structures and bank stabilization age and how richness and abundance of herbaceous plant, ground-beetle and benthic macro-invertebrate species, as well as multi-richness and multi-abundance, responded to changes in habitat quality and to broad-scale environmental variables (i.e., climate, hydrology and land-cover) that are known to greatly influence riparian biodiversity (e.g., Collier and Clements, 2011; Feld and Hering, 2007; Kail and Wolter, 2013). The decision was made to focus on richness and abundance patterns, because both metrics may highlight different aspects of ecosystem functioning, e.g., biotic interactions for species richness versus biomass production for total abundance (Soliveres et al., 2016). The three taxonomic groups were selected based on (i) their complementary response in terms of dispersal ability and (ii) their habitat requirements. Since cross-taxon congruence is of low consistency (Burrascano et al., 2018), the multi-taxonomic approach represents an opportunity to enhance our understanding of the human impacts on biodiversity, allowing us to better orient conservation and restoration strategies. Based on this approach, we explored the three following hypotheses: (i) soil bioengineering techniques through the active introduction of native tree species induce an increase in riparian habitat quality, which is expected to furthermore increase over time; (ii) related changes in riparian habitat quality induce an increase in the richness and abundance of terrestrial and aquatic species groups; (iii) the added-value of soil bioengineering techniques for biodiversity is mediated by broad-scales environmental factors (i.e., climate, hydrology and land-cover) which may greatly influence the response of multi-taxonomic diversity to riparian habitat quality.

2. Materials and Methods

2.1. Study area and sampling design

The study was carried out in the French and Swiss foothills of the Alps and Jura Mountains (Fig. 1), which are characterized by a limestone substratum and a temperate climate. We selected a large array of rivers (n = 23), between the Drôme River (44°43'N; 4°58'E) and the Doubs River (47°21'N; 7°10'E), at elevations ranging from 200 to 700 m asl. The watershed area at the sampling sites ranges from 5 to 5,700 km^2 and land cover is characterized by forested areas (48 %), agricultural areas (39 %), sparsely vegetated areas (8 %) and urban areas (5 %). All of the rivers studied belong to the same vegetation zone, i.e., "lower and mid-mountain: collinear and mountain 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, we sampled a total of 37 riverbank sites: 29 were engineered for erosion control and 8 were young natural riparian willow stands (Table A.1.). Among the engineered riverbank sites, four different stabilization structures were investigated: riprap protection (n = 8), mixed protection, i.e., riprap at lower part combined with soil bioengineering at the upper part of the bank (n = 7), vegetated crib wall (n= 6) and willow fascines (n= 8). All streambank protection occurred between 3 and 9 years prior to the study.

2.2. Biodiversity assessment

Along each riverbank site, two terrestrial species groups – vascular plants and ground-beetles - and one aquatic species group - benthic invertebrates - were sampled.

Plant species were surveyed following the Point Contact Method from May to July 2011. Plant species diversity and frequency were estimated using a 2m-long stick. Measurements were taken every meter along three 25 m transects located parallel to the riverbank (transect 1 near the water line, transect 2 in the middle of the bank and transect 3 at the top of the riverbank). All species were identified by the authors using floras.

Ground-beetles were collected on a subset of 34 riverbank sites in June 2011. At each of the sites, two pitfall traps were buried into the ground, 20 m away from each other. The traps had a diameter of 7 cm and were filled with a mixture of 50 % propylene glycol and 50 % water and detergent to kill and preserve the insects. All the ground-beetles trapped were identified to the species level by independent experts.

A surber sampler was used to sample benthic invertebrates – aquatic insects, shellfish, mollusks and worms (i.e., Platyhelminthes, Annelida and Nematoda) – in September and October 2011. To explore a representative range of habitats at each site, five surber samples (500 µm mesh size, sampling area of 1/20 m²) were taken in the five most qualitative submerged habitats (for details, see Cavaillé et al., 2018). The material collected was fixed in 70 % ethanol and sorted in laboratory. Benthic invertebrates were identified by independent experts to the lowest practical taxonomic level.

2.3. Riparian habitat variables

To assess the added value of soil bioengineering for riparian biodiversity, we used three terrestrial and three aquatic habitat variables that were expected to highlight differences in habitat quality among the four different stabilization structures plus natural willow stands and between recent and old structures. For the terrestrial part of riverbanks, we considered the richness and density of pioneer tree species (i.e., *Salix* spp., *Populus* spp. and *Alnus* spp.) as well as the density of others tree species recorded along the three transects. The focus was made on pioneer tree species because they are naturally widespread along mountain stream riverbanks, they are considered as river system engineers (Gurnell, 2014) and they support a wide range of animal species (Kennedy and Southwood, 1984; Newsholme, 1992). For the aquatic part of the bank, we considered the proportion of the submerged bank covered by the two dominant substrates, i.e., slabs (mean cover = 33.6%) and pebbles (mean cover = 41.8%) which respectively represent low and high potential habitats for macroinvertebrate species, along with an index of substrate quality, combining the proportion of each aquatic-microhabitat with a "habitability" note, ranking substrates in relation to their ability to host organisms. This was done by considering the following 12 substrate types: slab (Hab = 0), algae (Hab = 1), sand/silt (Hab = 2), mud (Hab = 3), helophyte (Hab = 4), gravel (Hab = 5), block (Hab = 6), pebble (Hab = 7), root (Hab = 8), litter (Hab = 9), hydrophyte (Hab = 10) and bryophyte (Hab = 11). Aquatic-microhabitats were considered because they are known to greatly influence benthic invertebrates (Cogerino et al., 1995; Verdonschot et al., 2016) but are rarely considered in restoration projects using soil bioengineering techniques, which mainly focus on the upper part of the riverbank.

Based on these six habitat quality variables, we built a synthetic index of riparian habitat quality using the first axis of a principal component analysis (PCA) that reflects the multivariate similarity of riverbank sites (Fig. A.2.). Decision was made to focus on the first PCA axis only because it best represented variations among stabilization structures (i.e., PCA second axis best represented variations within stabilization structures).

2.4. Broad-scale environmental variables

To validate our sampling design, we used spatial, topographical, climatic, hydrological and land cover variables (Table 1 and Fig. A.3.), in addition to the above-mentioned riparian habitat variables. Spatial – i.e., latitude, longitude – and topographical variables – i.e., altitude, slope gradient and sunlight exposure – were measured directly on each riverbank site using GPS, compass and inclinometer and were used to control for possible bias in sites distribution throughout the study area. Climatic, hydrological and land cover variables were used in models to account for important parameters that may structure biodiversity patterns but also to consider possible factors underlying the effect of riparian habitat variables. Climatic variables – i.e., mean annual air temperature and total annual precipitation – were derived from the WorldClim climatic model (Hijmans et al., 2005) and adjusted for the effect of altitude following Zimmermann and Kienast (1999). Hydrological variables – i.e., stream width and watershed area – were respectively assessed using a laser rangefinder and Digital Elevation Model analysis, by calculating flow direction grids and then delimiting individual drainage areas for each site along river networks with the GRASS GIS software (GRASS Development Team, 2017). Land cover variables – i.e., forest area proportion and urban area proportion in the surrounding landscape – were measured within a 500-m-radius around each riverbank site with the QGIS Geographic Information System (QGIS Development Team, 2015).

2.5. Statistical analyses

Analyses were performed with the R version 3.3.2 software (R Core Team, 2018). Independent continuous variables with a skewness >1 were log- or log+1-transformed to reach an approximately normal distribution, while for proportional data, logit transformation was applied. As independent factors we considered "riverbank protection techniques", a five levels factor distinguishing among riprap, mixed, crib wall, fascine and natural riverbank sites, and “age of the structure”, a three levels factor distinguishing among recent structures (i.e., 3 to 5 years old), old structures (i.e., 6 to 9 years old) and natural riverbanks.

To determine whether terrestrial and aquatic habitat variables, as well as the index of riparian habitat quality, varied among “techniques” and “age” factors, we used one-way ANOVAs with Tukey’s HSD post hoc tests.

To determine whether changes in riparian habitat quality among riverbank stabilization structures and bank stabilization age and in broad-scale environmental variables influence biodiversity patterns we used Linear Mixed Models (LMMs) and General Linear Mixed Models (GLMMs). As dependent variables, we used the pooled species richness or abundance of herbaceous plants, ground-beetles and aquatic macro-invertebrates, divided into: aquatic insects, shellfish, mollusks and worms, as well as an index of multi-taxonomic diversity (Allan et al., 2014). This diversity metric was calculated as the average scaled species richness or abundance per taxonomic group (i.e., relative to the maximum observed number of species or individuals from each group across all sites). The multi-diversity metric ranges between 0 and 1, with a value of 1 meaning that a site hosts all species contained in the study area species pool. It has the advantage of equally balancing the different taxa and of being comparable across sites, whatever the sampling effort (Allan et al., 2014). We developed 13 a priori biologically plausible candidate linear models, plus the null model, to verify hypothesis statements (Table A.4.) and used mixed-effect models with site proximity as a random effect. Site proximity, i.e., sites that belong to the same main river catchment within a 20-km radius, was used to account for spatial autocorrelation between the closest sites and because the study sites on the same riverbank were not real replicated. We fitted normal distribution LMMs for multi-richness and multi-abundance, Poisson distribution GLMMs for richness of each taxonomic group and Negative Binomial distribution GLMMs for abundance of each taxonomic group. Independence of climatic, hydrological and land cover variables from the index of riparian habitat quality were tested using linear models. The variance explained by the models was estimated with the marginal coefficient of determination for fixed effect parameters alone (Nakagawa and Schielzeth, 2013). In all candidate models, the variance inflation factor was below three, indicating a lack of collinearity issues (Dormann et al., 2013). To identify the most parsimonious regression model, we used the Akaike information criterion corrected for small sample sizes (Burnham and Anderson, 2002). Model averaging was used when the AICc weight of the top-ranking model was < 0.95. Average parameter estimates and associated unconditional standard errors were calculated from the subset of top-ranking models for which the sum of AICc weights reached > 0.95.

3. Results

3.1. How riparian habitat quality varied among riverbank stabilization structures and bank stabilization age

One-way ANOVA revealed that the index of riparian habitat quality varied significantly among riverbank protection techniques ($p < 0.001$) and among age classes ($p = 0.043$) (Fig. 2). Tukey HSD tests showed that the index of riparian habitat quality was significantly more important on crib wall, fascine and natural sites than on riprap and mixed sites. For the age factor, Tukey HSD tests revealed no significant differences. For terrestrial habitat variables, one-way ANOVAs revealed that the richness ($p < 0.001$) and density ($p < 0.001$) of pioneer tree species as well as the density of others tree species ($p = 0.005$) varied significantly among riverbank protection techniques but not among age classes (Fig. A.5.). Tukey HSD tests showed that the richness and density of pioneer tree species was significantly more important on mixed, crib wall, fascine and natural sites than on riprap sites and that richness only was significantly more important on fascine sites than on mixed sites. Also, the density of others tree species was significantly more important on mixed sites than on riprap, fascine and natural sites. For aquatic habitat variables, one-way ANOVAs revealed that the slab ($p < 0.001$) and pebble ($p = 0.019$) substrate proportions varied significantly among riverbank protection techniques, while only the slab substrate proportion ($p = 0.010$) varied significantly among age classes (Fig. A.5.). Tukey HSD tests showed that the proportion of slab was significantly more important on riprap, mixed and crib wall sites than on fascine and natural sites. Also, the proportion of slab was significantly more important on recent and old structures than on natural sites.

3.2. How diversity patterns responded to riparian habitat quality and broad-scale environmental variables

Overall, 64 ground-beetle species were recorded on the subset of 34 sites; while 189 herbaceous plant, 182 aquatic insect, 15 shellfish, 28 mollusk and 32 worm taxa were recorded on all 37 sites, resulting in a dataset of 510 taxa.

Linear models showed that the variation in spatial, topographical, climatic, hydrological and land cover variables was not related to the index of riparian habitat quality (Table A.6.). This indicates that environmental factors varied consistently along the five types of riverbank sites and that, in our study design, environmental factors were independent from the synthetic index developed. Only riverbank slope gradient decreased significantly with an increase of index values.

LMM results showed that multi-taxonomic diversity was best predicted by models accounting for the index of riparian habitat quality (Table 2). GLMM results showed that the richness of aquatic insect, mollusk and worm species and the abundance of plant species were also best predicted by models accounting for the index. Models accounting for climatic variables only best predicted the richness of shellfish species; models accounting for hydrological variables only best predicted the richness of ground-beetle species and the abundance of ground-beetle, shellfish and worm species; models accounting for land cover variables only best predicted the richness of plant species and the abundance of aquatic-insect and mollusk species. Although some of the models seemed quite robust for explaining biodiversity patterns, model selection uncertainty still remains (Fig. 3 & Fig. A.7.). We therefore used model averaging, from the 2 to the 12 best models, to draw inferences about how much the variables influenced diversity patterns.

Multi-richness, aquatic insect and worm richness and plant abundance increased significantly with increasing values for the index of riparian habitat quality (Table 3). For climatic variables, only mollusk richness increased significantly with increasing values for temperature while multi-richness and mollusk richness decreased significantly with increasing values for annual precipitation. For hydrological variables, multi-abundance, aquatic-insect, shellfish and worm abundance decreased significantly with increasing values for stream width, while ground-beetle richness increased significantly. Moreover, shellfish abundance decreased significantly with increasing values for watershed area, while ground-beetle and mollusk richness increased significantly. For land cover variables, multi-richness and mollusk richness and abundance decreased significantly with an increasing proportion of urban area in the surrounding landscape, while plant richness and aquatic insect richness and abundance increased significantly with an increasing proportion of forest area in the surrounding landscape.

4. Discussion

Our results clearly show that multi-taxonomic diversity increased with increasing values of riparian habitat quality on riverbanks. Though the significance of the index developed varied among taxonomic groups, the effect on diversity patterns was consistent. These findings support the idea that (i) the active introduction of native tree species enhances riparian habitat quality over time for biodiversity, and that (ii) soil bioengineering techniques, especially willow fascines and to lower extend vegetated crib wall, can be a good compromise solution to support both erosion control and biodiversity conservation.

4.1. Soil bioengineering techniques enhance riparian habitat quality for biodiversity

Consistently with our first hypothesis, we found that soil bioengineering techniques enhanced the habitat quality of both terrestrial and aquatic compartments. Thus, our results indicate that willow fascines and vegetated crib wall, i.e. soil bioengineering techniques, allowed for a greater richness and density of pioneer tree species but also for a larger cover of high quality aquatic micro-habitats, i.e., better able to host organisms. Reversely, riprap and mixed protection, i.e. civil engineering techniques, were associated with an increase in non-pioneer tree species richness, among which the shrubs species *Buddleia davidii*, *Cornus sanguinea* and *Ligustrum vulgare* dominated, and with an oversimplification in aquatic-microhabitats, which was due to an artificially increase in the proportion of slabs on the submerged part of the bank. Globally, our results pointed out the multivariate similarity, on the one hand, between stabilization structures made of willow fascines and natural riparian willow stands and, on the other hand, between riprap structures and mixed protections (see also Fig. A.2.). This highlights the importance of including not only the upper part of the riverbank but also the lower submerged part when designing restoration projects. Riverbank protection techniques combining artificial riprap on the lower part of the bank and bioengineering structures on the upper part of the bank appear to be poor restoration solutions for aquatic biodiversity (Cavaillé et al., 2018), even though positive effects on terrestrial plant diversity have been highlighted (Cavaillé et al., 2015). River managers wishing to restore both the terrestrial and the aquatic biodiversity should therefore promote substrate heterogeneity along the lower part of the riverbank and maintain or restore native tree cover along the upper part of the riverbank. Overall, our results confirm that soil bioengineering techniques can increase the habitat quality of degraded riverbanks (Li and Eddleman, 2002), first, by accelerating the colonization and establishment of native species (e.g., Holl and Crone, 2004; McClain et al., 2011), second, by increasing the overall quality and diversity of wildlife habitats (e.g., Li et al., 2006; Sudduth and Meyer, 2006). This effect may be related to the active introduction of ecosystem engineer species (Gurnell, 2014), such as *Salix viminalis*, *S. puprurea* or *S. triandra* in our study area, which are able to rapidly respond to the physical riparian environment by modifying local ecological conditions (e.g., water temperature, sunshine or flow conditions), by increasing physical interactions with sediment load (Corenblit et al., 2009) and thus by favouring greater environmental heterogeneity (Gurnell et al., 2012).

As expected, the increase in both terrestrial and aquatic habitat quality was related to an increase in both terrestrial and aquatic species richness and abundance. Indeed, we found that the synthetic index of riparian habitat quality developed had a consistent effect among taxa, i.e., the richness and abundance of all the taxonomic groups increased positively with increasing values of the index and significantly for several species groups and the multi-richness. Thus, in accordance with the few available studies (e.g., Cavaillé et al., 2013; Li et al., 2006; Sudduth and Meyer, 2006), our results pointed out a positive relationship between soil bioengineering techniques and riparian biodiversity. This result confirms that the active introduction of pioneer tree species, may facilitate the establishment of terrestrial and aquatic species and thus promote biodiversity along riparian zones (Gurnell, 2014). Moreover, the use of willow species, i.e., native pioneer species characteristic of European riverbanks, in soil bioengineering techniques such as vegetated crib wall and fascines may also promote positive biotic interactions by providing shelter and resources for a wide range of species (Newsholme, 1992). For example, it has been showed that *Populus* spp. and *Salix* spp. enhanced fine sediment retention, which increased seed retention of hydrochorous species and favored greater riparian plant diversity (Corenblit et al., 2016). Additionally, our results showed that benthic macroinvertebrates were significantly influenced by the index of riparian habitat quality. This confirms the importance of high quality substrates for aquatic biodiversity (Cogerino et al., 1995; Verdonschot et al., 2016) and the fact that artificial substrata resulting from civil engineering techniques can reduce the taxonomic and functional diversity of benthic invertebrates (Feld and Hering, 2007). Overall, we infer that soil bioengineering techniques may promote the self-organizing ability of riparian ecosystems, leading toward the desired target of stable community development over time.

4.2. Broad-scale environmental variables mediate the positive effects that soil bioengineering techniques have on riparian biodiversity

Beside the effect of riparian habitat quality on biodiversity, our results showed that diversity patterns were obviously influenced by environmental factors at larger scales, which mediated the added-value of soil bioengineering techniques for biodiversity. For climatic variables, the negative effect that annual precipitation had on multi-richness may be related to an increase in water flow velocity for streams located at higher elevations (altitude/precipitation, $r = 0.86$). Indeed, water flow velocity may induce temporal variations in the diversity of benthic organisms, but also in that of terrestrial arthropods through occasional flooding (e.g., Lafage et al., 2015). These deleterious effects may be exacerbated in mountainous areas by the influence of stream slope. Moreover, since precipitation and temperature are closely related ($r = -0.72$), this effect may also mask the influence that colder environments have on stream invertebrate assemblages, i.e., a decrease in diversity with altitude (Jacobsen et al., 1997). For hydrological variables, negative effects on both the richness and abundance of several taxonomic groups were found. Specifically, multi-abundance decreased significantly with increasing values for stream width. Given the sensibility of benthic macro-invertebrate species to aquatic habitat quality (Cogerino et al., 1995; Verdonschot et al., 2016), we inferred that the negative effect of hydrological factors reported herein may be attributed to changes in water physical proprieties (e.g., turbidity, dissolved oxygen) and/or in terrestrial and aquatic-microhabitats (e.g., sedimentation, homogenization) with increasing stream width and watershed area. Indeed, in our study area, the largest rivers (e.g., the Rhône, Isère and Arve Rivers) are located in industrialized valleys or in intensive farming areas and are more likely to be subject to channeling. The negative effects of human activities on riparian biodiversity are even more confirmed by the fact that multi-richness decreased with an increase in the proportion of urban areas in the surrounding landscape. This negative effect of human occupation on riparian biodiversity has already been well documented for multiple taxa (Feld and Hering, 2007; Moore and Palmer, 2005; Paul and Meyer, 2001) and our results confirm these previous findings. Specifically, this showed that stabilization structures made of willow fascines or vegetated crib wall cannot solve environmental degradations due to human activity in the vicinity of riparian zones. Reversely, we found that herbaceous plant richness increased concomitantly with an increase in the proportion of forest areas in the surrounding landscape, which is consistent with the positive overstory-understory relationship that had been previously reported in forest ecosystems (e.g., Ingerpuu et al., 2003; Mölder et al., 2008). Also, we found that the richness and abundance of aquatic-insects, among which Ephemeroptera, Plecoptera and Trichoptera represented 44 % of the total richness and 54 % of the total abundance, significantly increased with forest cover in the surrounding landscape. Given the sensitivity of these taxa to water quality, this result may confirm the effectiveness of riparian forest buffer filters in improving water quality (e.g., Lowrance et al., 1997; Osborne and Kovacic, 1993). Overall, our findings highlight the importance of considering multiple-scale environmental factors when analyzing diversity patterns in riparian zones (Collier and Clements, 2011; Feld and Hering, 2007; Kail and Wolter, 2013). This is all the more true for studies encompassing a wide range of ecological conditions as it was the case for our study in the French and Swiss foothill of the Alps and Jura Mountains.

5. Conclusions

We found that soil bioengineering techniques are a good compromise between erosion control and biodiversity conservation. However, given that the erosion control performance of these techniques have been rarely investigated (e.g., Fernandes and Guiomar, 2016), we call for more research to better understand the optimal balance between erosion and conservation in riparian zones (Stokes et al., 2014). Also, it should be reminded that riverbank stabilization impedes bank erosion, which is a natural geomorphic process that promotes dynamic habitats for riparian biodiversity (Florsheim et al., 2008). River managers should therefore firstly allow bank erosion processes to operate, secondly promote soil bioengineering techniques if important human stakes are threatened by erosion. Beyond the influence of local habitat variables, we found that broad-scale environmental variables shape diversity patterns. This indicates that the full added value of soil bioengineering techniques for biodiversity will only become apparent if more attention is paid to mitigating the negative impact of human-induced environmental changes and if larger scale environmental parameters are taken into account as early as possible in restoration project (Rey et al., 2019). Finally, the strong variation in the response of taxonomic groups to environmental variables that we found suggest that restoration success should not be evaluated based on the interpretation of a single taxonomic group (e.g., Johnson et al., 2006). Integrated measurements of biodiversity seem best suited because they identify conditions that simultaneously maximize the diversity of multiple taxonomic groups.

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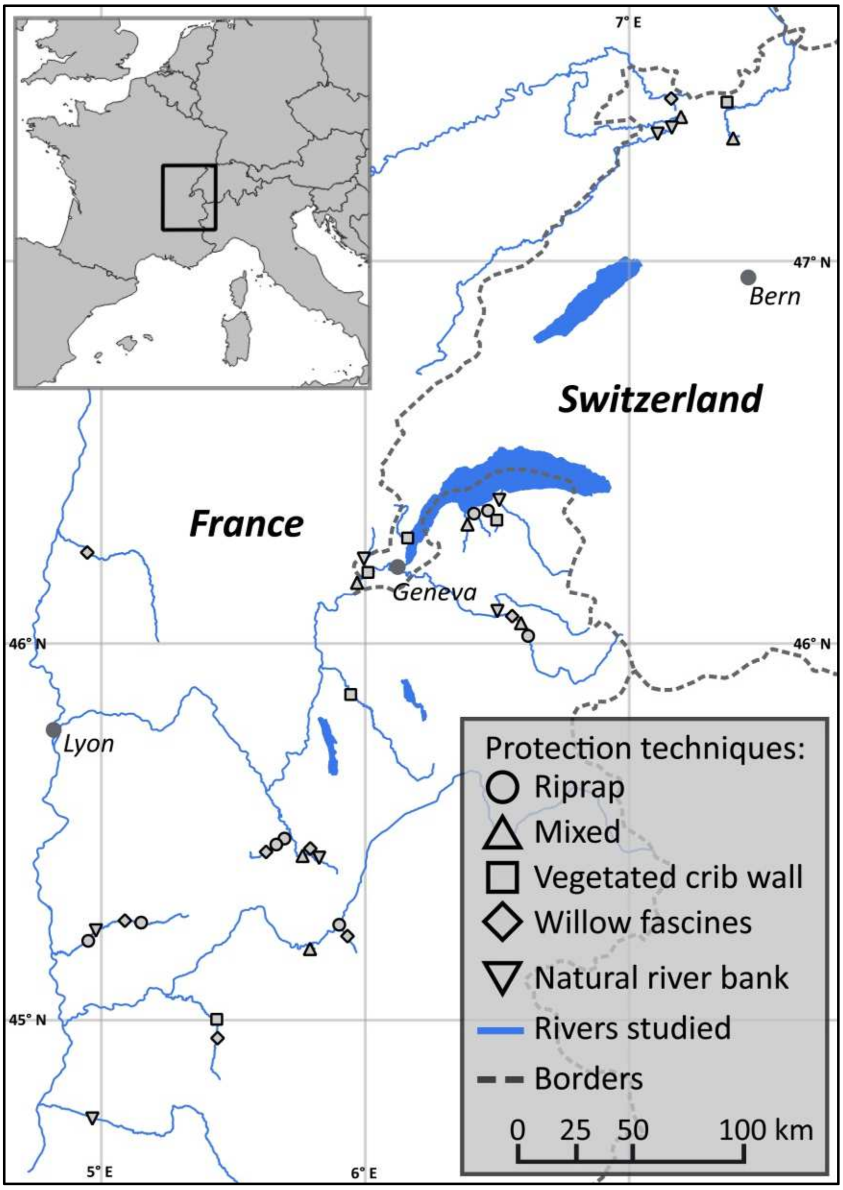
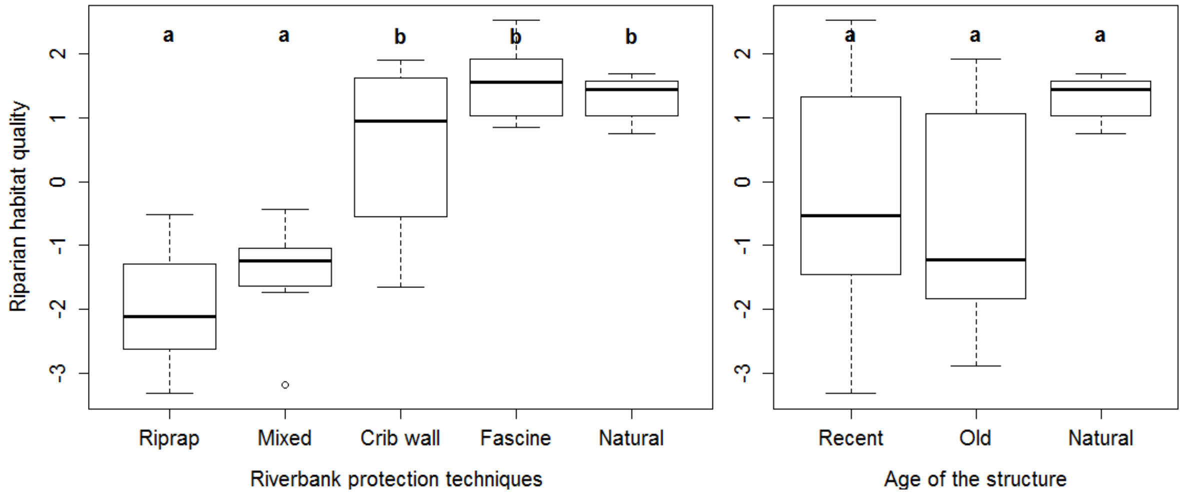


Fig. 1. Study area and distribution of rivers and sites sampled for riverbank protection techniques in the foothills of the Alps and Jura Mountains (France and Switzerland).

Fig. 2. Variation of the index of riparian habitat quality, i.e., PCA first axis combining three terrestrial and three aquatic habitat variables, in relation to riverbank protection techniques factor and the age of the stabilization structure factor. Bold letters indicate significance differences between factor levels based on Tukey's HSD post hoc test.



674 **Fig. 3.** Top-ranked LMMs predicting multi-richness and multi-abundance along different riverbank stabilization structures of different ages, plus natural riparian willow stands, along a gradient of increasing riparian habitat quality in the foothills of the Alps and Jura Mountains (France and Switzerland).

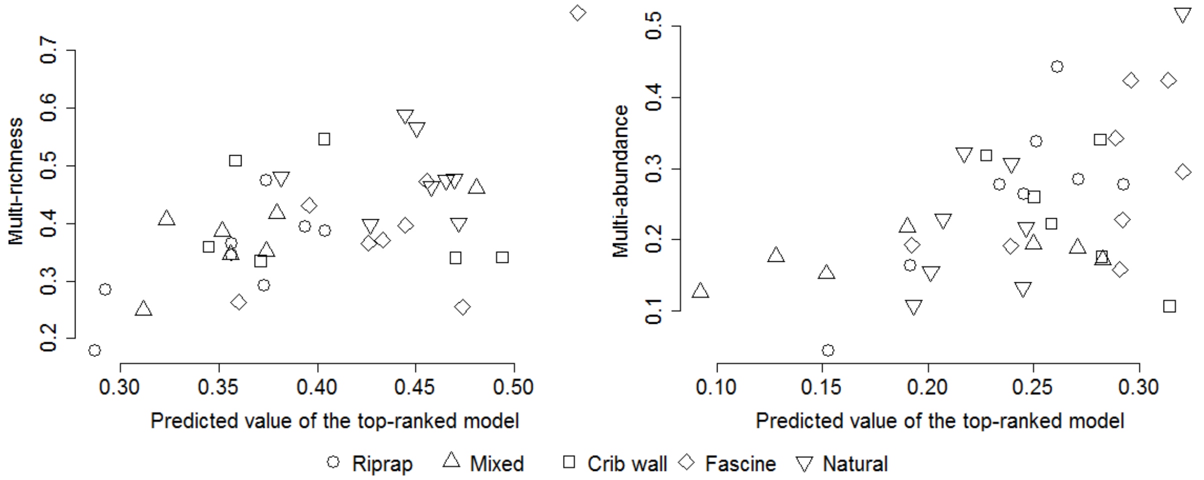


Table 1. Description of environmental variables used to model multi-taxonomic diversity patterns along different riverbank stabilization structures of different ages, plus natural riparian willow stands, in the foothills of the Alps and Jura Mountains (France and Switzerland).

Variables	Description	mean (±SD)	Range
Spatial and topographical variables			
Lati	Latitude in decimal degrees	45.98 (±0.77)	44.73 - 47.41
Long	Longitude in decimal degrees	6.08 (±0.71)	4.95 - 7.39
Alti	Altitude in meters	396 (±116)	161 - 700
Slope	Slope gradient in percentage	58.4 (±33.8)	12 - 152
Expo	Sunlight exposure in degrees	137.43 (±97.76)	0 - 315
Riverbank habitat variables			
Habitat_Quality	Index of riparian habitat quality	0.00 (±1.71)	-3.32 - 2.52
Terrestrial part of the bank:			
Rich_Pioneer	Richness of pioneer tree species	4.14 (±2.25)	0 - 9
Dens_Pioneer	Density of pioneer tree species	87.43 (±69.67)	0 - 282
Dens_Others	Density of others tree species	18.95 (±24.10)	0 - 97
Aquatic part of the bank:			
Subst_Quality	Substrate quality index	131.27 (±170.87)	15 - 780
Prop_Slab	Slab microhabitat proportion (%)	33.62 (±38.80)	0 - 96
Prop_Pebble	Pebble microhabitat proportion (%)	41.84 (±37.24)	0 - 96
Broad-scale environmental variables			
Climatic variables:			
Temp	Mean annual temperature (°C)	10.32 (±0.87)	8.95 - 12.41
Precip	Sum annual precipitation (mm)	1802 (±87)	1580 - 1961

Hydrological variables:			
Stream_W	Stream width (m)	20.29 (±23.12)	3.00 - 107.00
Watershed	Watershed area (km²)	512 (±1106)	4.4 - 5761.2
Land cover variables			
Prop_Forest	Forest proportion (%, 500 m radius)	25.64 (±13.63)	0.00 - 54.85
Prop_Urban	Urban area proportion (%, 500 m radius)	17.83 (±20.87)	0.17 - 62.94

Table 2. Top-ranking models among 14 a priori models predicting terrestrial and aquatic species richness and abundance along different riverbank stabilization structures of different ages, plus natural riparian willow stands, in the foothills of the Alps and Jura Mountains (France and Switzerland), as assessed with the Akaike information criterion corrected for small sample size (AICc). Number of estimated parameters including the intercept and random effect (k), AICc, AICc weight (*W*) and marginal coefficient of determination for fixed effect (R^2_{GLMM}) are provided (Independent variables are defined in Table 1).

Dependent variable	Model (fixed-effects)	k	AICc	*W*	R^2_{GLMM}
Multi-richness	Habitat_Quality + Prop_Urban	5	-61.0	0.387	0.304
Mutli-abundance	Habitat_Quality + Stream_W	5	-63.4	0.485	0.282
Plant richness	Prop_Forest	3	257.5	0.488	0.143
Plant abundance	Habitat_Quality	4	414.9	0.316	0.175
Ground-beetle richness	Watershed	3	167.9	0.604	0.228
Ground-beetle abundance	Watershed	4	226.0	0.150	0.096
Aquatic-insect richness	Habitat_Quality + Prop_Forest	4	298.2	0.94	0.357
Aquatic-insect abundance	Prop_Forest	4	568.5	0.516	0.228
Shellfish richness	Precip	3	134.3	0.202	0.081
Shellfish abundance	Stream_W	4	579.4	0.672	0.422
Mollusk richness	Habitat_Quality + Precip	4	154.9	0.299	0.262
Mollusk abundance	Prop_Urban	4	390.6	0.268	0.167
Worm richness	Habitat_Quality	3	177.6	0.296	0.174
Worm abundance	Stream_W	4	479.5	0.325	0.124

Table 3. Average coefficients (AC, mean ±SD) and confidence intervals (95% CI) for each variable predicting terrestrial and aquatic species richness and abundance along different riverbank stabilization structures of different ages, plus natural riparian willow stands, in the foothills of the Alps and Jura Mountains (France and Switzerland). The 95% confidence interval of coefficients in bold excluded 0.

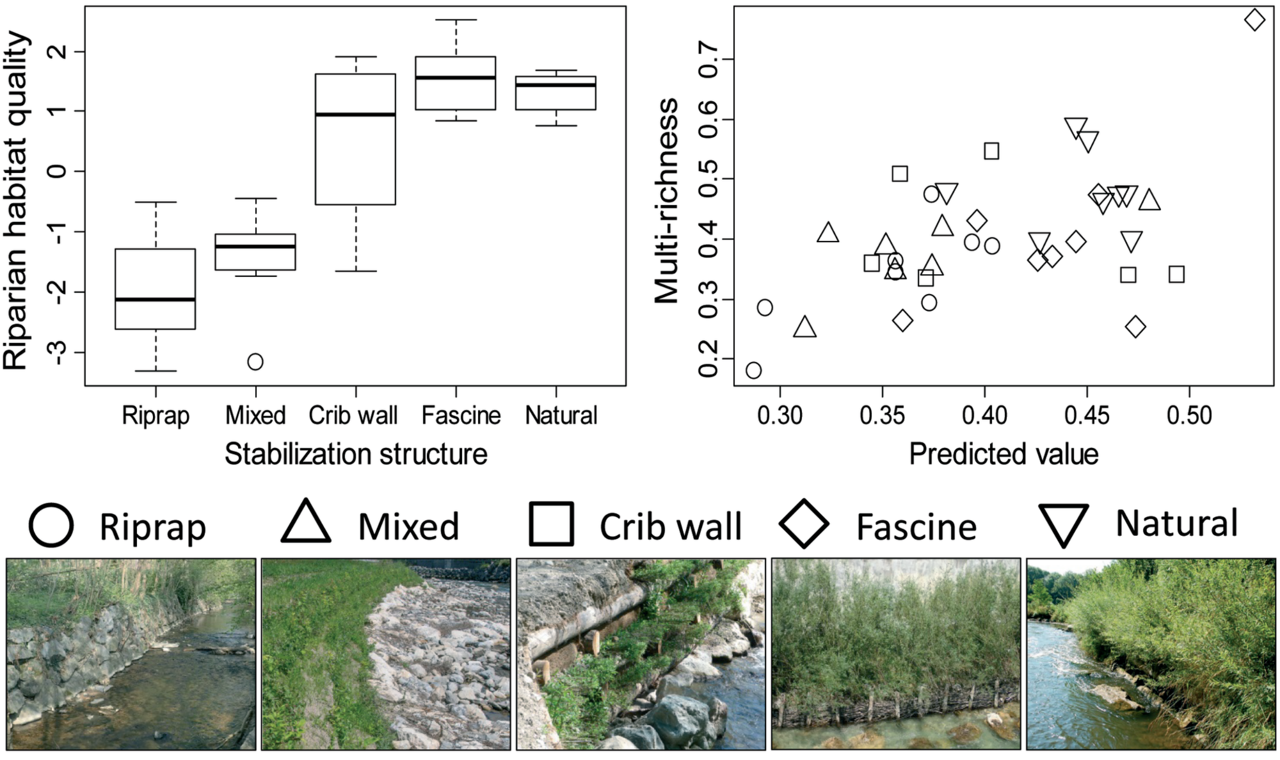
Dependent variable	Habitat_Quality		Temp		Precip		Stream_W	
	AC	95% CI	AC	95% CI	AC	95% CI	AC	95% CI
Multi-richness	**0.021 (±0.010)**	**(0.001; 0.040)**	0.036 (±0.019)	(-0.001; 0.073)	**-0.041 (±0.018)**	**(-0.077; -0.006)**	NA	NA
Multi-abundance	0.016 (±0.009)	(-0.002; 0.033)	0.025 (±0.020)	(-0.015; 0.064)	NA	NA	**-0.047 (±0.015)**	**(-0.077; -0.017)**
Plant richness	0.004 (±0.026)	(-0.046; 0.054)	-0.087 (±0.058)	(-0.200; 0.026)	0.056 (±0.053)	(-0.048; 0.159)	-0.008 (±0.043)	(-0.092; 0.076)
Plant abundance	**0.112 (±0.043)**	**(0.029; 0.196)**	0.026 (±0.081)	(-0.133; 0.186)	-0.066 (±0.070)	(-0.203; 0.070)	0.000 (±0.071)	(-0.139; 0.139)
Ground-beetle richness	0.030 (±0.058)	(-0.083; 0.143)	NA	NA	NA	NA	**0.297 (±0.101)**	**(0.099; 0.494)**
Ground-beetle abundance	0.121 (±0.105)	(-0.086; 0.327)	0.207 (±0.211)	(-0.206; 0.620)	-0.180 (±0.147)	(-0.468; 0.107)	0.063 (±0.207)	(-0.342; 0.469)
Aquatic-insect richness	**0.051 (±0.019)**	**(0.014; 0.089)**	NA	NA	NA	NA	NA	NA
Aquatic-insect abundance	0.012 (±0.079)	(-0.143; 0.167)	0.106 (±0.182)	(-0.250; 0.462)	-0.071 (±0.160)	(-0.384; 0.243)	**-0.265 (±0.152)**	**(-0.564; 0.034)**
Shellfish richness	0.051 (±0.061)	(-0.067; 0.170)	0.160 (±0.113)	(-0.062; 0.382)	-0.169 (±0.097)	(-0.359; 0.021)	0.031 (±0.098)	(-0.161; 0.223)
Shellfish abundance	0.080 (±0.108)	(-0.131; 0.291)	NA	NA	NA	NA	**-0.975 (±0.216)**	**(-1.397; -0.552)**

Mollusk richness	0.105 (±0.065)	(-0.024; 0.233)	**0.424 (±0.202)**	**(0.027; 0.820)**	**-0.412 (±0.153)**	**(-0.711; -0.113)**	NA	NA
Mollusk abundance	0.196 (±0.189)	(-0.175; 0.567)	0.927 (±0.607)	(-0.262; 2.117)	-0.927 (±0.580)	(-2.063; 0.210)	-0.114 (±0.468)	(-1.031; 0.803)
Worm richness	**0.106 (±0.043)**	**(0.022; 0.191)**	0.056 (±0.079)	(-0.098; 0.210)	-0.039 (±0.068)	(-0.172; 0.095)	-0.018 (±0.071)	(-0.158; 0.122)
Worm abundance	0.037 (±0.081)	(-0.122; 0.196)	-0.055 (±0.159)	(-0.367; 0.258)	0.142 (±0.116)	(-0.086; 0.370)	**-0.272 (±0.129)**	**(-0.525; -0.018)**

Table 3. Continued

Dependent variable	Watershed		Prop_Urban		Prop_Forest	
	AC	95% CI	AC	95% CI	AC	95% CI
Multi-richness	NA	NA	**-0.025 (±0.009)**	**(-0.043; -0.007)**	0.015 (±0.022)	(-0.028; 0.058)
Multi-abundance	-0.007 (±0.009)	(-0.025; 0.010)	-0.012 (±0.009)	(-0.031; 0.007)	NA	NA
Plant richness	-0.020 (±0.023)	(-0.064; 0.024)	0.006 (±0.028)	(-0.049; 0.061)	**0.132 (±0.056)**	**(0.022; 0.242)**
Plant abundance	0.020 (±0.039)	(-0.057; 0.096)	0.005 (±0.039)	(-0.072; 0.081)	0.029 (±0.095)	(-0.157; 0.215)
Ground-beetle richness	**0.175 (±0.051)**	**(0.075; 0.275)**	NA	NA	NA	NA
Ground-beetle abundance	0.173 (±0.106)	(-0.035; 0.381)	-0.144 (±0.100)	(-0.339; 0.052)	-0.199 (±0.314)	(-0.815; 0.416)
Aquatic-insect richness	NA	NA	NA	NA	**0.287 (±0.056)**	**(0.176; 0.397)**
Aquatic-insect abundance	-0.060 (±0.086)	(-0.228; 0.107)	-0.053 (±0.095)	(-0.240; 0.134)	**0.548 (±0.200)**	**(0.156; 0.940)**
Shellfish richness	0.036 (±0.054)	(-0.070; 0.142)	-0.078 (±0.055)	(-0.186; 0.030)	-0.047 (±0.123)	(-0.289; 0.194)
Shellfish abundance	**-0.479 (±0.133)**	**(-0.739; -0.218)**	NA	NA	NA	NA
Mollusk richness	**0.138 (±0.064)**	**(0.013; 0.263)**	**-0.191 (±0.089)**	**(-0.365; -0.016)**	NA	NA
Mollusk abundance	0.175 (±0.224)	(-0.264; 0.613)	**-0.505 (±0.253)**	**(-1.001; -0.010)**	0.542 (±0.580)	(-0.594; 1.678)
Worm richness	0.015 (±0.038)	(-0.060; 0.091)	-0.038 (±0.040)	(-0.117; 0.040)	-0.008 (±0.088)	(-0.182; 0.165)

Worm abundance	-0.108 (±0.077)	(-0.259; 0.044)	-0.005 (±0.074)	(-0.150; 0.141)	-0.170 (±0.175)	(-0.514; 0.174)



Riparian habitat quality
2
1
0
-1
-2
-3
Riprap
Mixed
Crib wall
Fascine
Natural
Stabilization structure
Multi-richness
0.7
0.6
0.5
0.4
0.3
0.2
0.30
0.35
0.40
0.45
0.50
Predicted value
Riprap
Mixed
Crib wall
Fascine
Natural