

# Vegetation of natural and stabilized riverbanks and early effects of removal of bank fixation

Carolin Seele-Dilbat<sup>1,2</sup> | Lena Kretz<sup>1,2</sup>  | Christian Wirth<sup>1,3,4</sup>

<sup>1</sup>Life Science, Systematic Botany and Functional Biodiversity, University Leipzig, Leipzig, Germany

<sup>2</sup>Department Conservation Biology, Helmholtz Centre for Environmental Research (UFZ), Leipzig, Germany

<sup>3</sup>German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany

<sup>4</sup>Max Planck Institute for Biogeochemistry, Jena, Germany

## Correspondence

Carolin Seele-Dilbat, University Leipzig, Life Science, Systematic Botany and Functional Biodiversity, Johannisallee 21-23, 04103 Leipzig, Germany.  
Email: [carolin.seele@uni-leipzig.de](mailto:carolin.seele@uni-leipzig.de)

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## Abstract

The majority of rivers in Europe has been dramatically altered in terms of their morphology and hydrology with severe consequences for the diversity and ecological functioning of the rivers and their floodplains. Consequently, an increasing number of river reaches has been restored over the past decades, often including the removal of bank fixation to reinitiate bank erosion and allowing for a widening of the rivers' cross-section. However, monitoring in detail the effect of such a measure on riverine vegetation is scarce. Using a Before-After-Control-Impact (BACI) design, we analysed the early changes of the vegetation 2 years after the removal of bank fixation at the Mulde River (central Germany). The results were compared with two types of control sites, representing a nonrestored as well as a natural riverbank that has never been fixed. We analysed differences in taxonomic and functional composition of the vegetation between bank types as well as community turnover after restoration. Two years after restoration, the vegetation differed clearly from the nonrestored sites. A substantial proportion of the community, especially the newly established species, became more similar to the natural bank community. Most importantly, spatiotemporal heterogeneity of the vegetation increased after removal of bank fixation, being an indicator for re-established dynamic processes similar to the natural site. The presented data serve as a baseline for a long-term monitoring and quantitative meta-analysis of restoration effects.

## KEYWORDS

diversity, plants, restoration, river, traits

## 1 | INTRODUCTION

Riverbanks are transitional boundaries (ecotones), between aquatic and terrestrial ecosystems. Under natural conditions, they are characterized by a high physical and biological heterogeneity and harbour a substantial proportion of the riparian diversity (Gregory et al., 1991; Naiman et al., 2005; Ward, 1998). However, worldwide

riverbanks face severe anthropogenic impacts by both hydrological (flow and flood control, disrupted continuity) and morphological modifications (channelization, embankments) (Tockner & Stanford, 2002). Frequently, riverbanks are stabilized with artificial bank protection measures to prevent bank erosion, with riprap (blocks of stones or crushed rock) being the most common material used for stabilization (Fischenich, 2003; Reid & Church, 2015). In Germany, approximately

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80% of riverbanks along national waterways are stabilized (Symmank et al., 2020).

Riverbank stabilization induces profound alterations of many structural characteristics and functions such as erosion and sedimentation processes, morphological bank evolution and riparian succession and alters the physical environment (Fischenich, 2003; Reid & Church, 2015). It thus affects habitat quality for biological communities (Florsheim et al., 2008). Ripraps substantially differ from the natural bank substrate and natural bank inclination and alter the land-water margin (Fischenich, 2003). Due to their rocky structure, ripraps heat up easily and show strong temperature fluctuations in summer, causing local differences in microclimate that favour thermophilic species at sites that would naturally be defined by high water availability (Cavaillé et al., 2013). Thus, ripraps account for distinct shifts in riverbank species composition for several aquatic, semi-aquatic and terrestrial groups (Fischenich, 2003; Florsheim et al., 2008; Reid & Church, 2015 and references therein).

In the natural state, riverbank vegetation occupies a highly dynamic area that is defined by frequent water level fluctuations and disturbances by floods (natural disturbance regime; Ward, 1998), which require special traits of plant species to cope with these conditions (Gregory et al., 1991), for example, physiological and morphological adaptations (Glenz et al., 2006; Voesenek & Bailey-Serres, 2015) and adaptations of life strategies (Naiman & Décamps, 1997). Besides high temporal dynamics, natural banks provide a high spatial heterogeneity of physical conditions with a variable moisture regime at different elevation zones along the bank gradient that are exposed to different flood frequencies, durations, and magnitudes (Naiman et al., 2005). This temporal and spatial heterogeneity of habitat conditions creates diverse niches and a high spatial and temporal beta diversity of vegetation (Anderson et al., 2011; Cook et al., 2018). In contrast, at stabilized banks, reduced bank erosion diminishes habitat dynamics that induce a shift to more stable communities with a lower spatial and temporal beta diversity. Under these conditions typical 'riverbank specialists' decline in favour of more common terrestrial species (Harvolk et al., 2015; Wolny et al., 2019) and the competitive structure changes in favour of competitive species, again promoting homogeneity in species composition (Walsh et al., 2005). The decline of highly adapted species and the increase of less specialized species is a widespread phenomenon along regulated rivers (Harvolk-Schoening et al., 2014; Walsh et al., 2005).

The ecological importance of bank erosion as an integral part of the functioning of river systems is increasingly recognized (Florsheim et al., 2008). Consequently, riverbank restoration and the removal of riprap have gained importance during the past decades (Morandi et al., 2017; Symmank et al., 2020). Although riverbank restoration is widely applied and its effects are monitored for several organism groups (Kail et al., 2015; Pilotto et al., 2019), the effectiveness of restoration remains debated (Bauer et al., 2018; Morandi et al., 2014; Roni et al., 2019; for discussion, see Schulz-Zunkel & Seele-Dilbat et al. this issue). Further, the methodologies for monitoring vary widely across projects (Bash & Ryan, 2002; Kail et al., 2015) hampering generalizations. Frequently a Before-After-Control-

Impact design (BACI, Smith, 2002; Stewart-Oaten et al., 1986, 1992) is used to measure restoration effects by comparing pre- and posttreatment conditions in restored and nonrestored control sites. For the majority of studies, the control sites represent the prerestoration condition (Bauer et al., 2018; Göthe et al., 2016; Kail et al., 2015; Modrak et al. 2017; Pilotto et al., 2019), but none of these studies included a river reach without anthropogenic modifications as a natural control site. Including a natural control site in the BACI design allows to measure, if the restored site becomes more similar to the natural state, in addition to measuring its difference from unrestored conditions. Including both control types (natural control and unrestored control) allows for a more comprehensive evaluation of the restoration effect.

We analysed the early effects of riverbank restoration on riparian vegetation 2 years after the removal of riprap in comparison to a natural site, that has never been fixed before, and a site with bank fixation at the River Mulde, Germany. Riparian vegetation is an important indicator that responds strongly and rapidly to changes in site conditions (Jähnig et al., 2009; Januschke et al., 2014; Modrak et al., 2017) and positive responses to restoration have been frequently reported (Göthe et al., 2016; Lorenz et al., 2018; Pilotto et al., 2019). We analysed changes in taxonomic and functional community composition as well as the spatial and temporal beta diversity of taxonomic and functional composition of the vegetation. For analyses of functional community composition, we focused on Grime's CSR (competitor, stress tolerator, and ruderal) strategies, as they are an aggregated measure of various traits capturing essential components of plant form and function (Díaz et al., 2016) with three main directions of adaptive specialization (see Pierce et al., 2013). According to Grime's CSR theory (Grime, 1974, 2001), competitors use large size and morphological plasticity to increase productivity in stable habitats without disturbances. In contrast, ruderals invest primarily in rapid growth rates and in high reproduction with a short life span to avoid frequent disturbances. Stress tolerators are slow-growing plants that maximize investment in physiological and morphological adaptation to maintain metabolic processes in resource-poor habitats.

As removal of bank fixation re-initiates bank erosion and sedimentation, our aim is to analyse how the restored site is recolonized with vegetation early after the impact (restoration) and to compare this process with patterns of vegetation succession at the natural and the stabilized riprap sites. Using functional information helps us to identify mechanisms of recolonization and to draw comparisons between sites (Fournier et al., 2015; Pilotto et al., 2019).

We address the following hypothesis:

1. After restoration, spatial heterogeneity and temporal turnover at the restored bank are higher compared to the nonrestored stabilized bank and more similar to the natural bank.
2. The higher disturbance level at the natural bank results in a higher proportion of ruderals, whereas more stable conditions at the stabilized bank result in a higher proportion of competitors. After restoration, mainly ruderal species recolonize the restored bank.

3. As the higher disturbance level at the natural bank requires a higher level of species specialization and functional differentiation, the natural bank is characterized by a higher functional diversity (richness, dispersion) and a higher functional uniqueness compared to the stabilized banks. After restoration functional diversity and uniqueness significantly increase.

## 2 | MATERIALS AND METHODS

### 2.1 | Study area

The study area was located along the Mulde River in Saxony-Anhalt (Central Germany). The Mulde River is a low-mountain-range river with periodic high water levels in spring, autumn and winter with a mean discharge of  $66.7 \text{ m}^3 \text{ s}^{-1}$  (gauging station 'Priorau 560090'). The studied river reach ( $51^\circ 43' - 46' \text{ N}$ ,  $12^\circ 17' - 18' \text{ E}$ ) is part of the UNESCO Biosphere Reserve 'River Landscape Elbe' and only moderately modified by hydro-engineering and without shipping infrastructures. However, about 75% of the riverbanks are stabilized by riprap (Puhlmann, 1997). Further, it is affected by a strong sediment loss, as large amounts of sediments get trapped in a water reservoir 22 km upstream causing severe riverbed deepening. Within the study area, natural and managed river reaches occur. At natural reaches, riverbanks were not modified by anthropogenic impacts (riprap, groynes), allowing the formation of pronounced cut banks and slip-off slopes by dynamic erosion and sedimentation processes. At managed reaches, cut banks were stabilized with ripraps to reduce riverbank erosion, resulting in very stable site conditions also at slip-off slopes.

During the study period (2016–2020) two high-discharge events occurred, one in February 2017 with overbank flow conditions (discharge peak  $353 \text{ m}^3 \text{ s}^{-1}$ ) and second in January 2019 with bankfull conditions (discharge peak  $286.6 \text{ m}^3 \text{ s}^{-1}$ ). Additionally, during the study period, three consecutive exceptional drought years occurred with a discharge lower than the long-term minimum discharge ( $12.5 \text{ m}^3 \text{ s}^{-1}$ ) for several months during the years 2018, 2019 and 2020.

### 2.2 | Study design

Effects of the removal of ripraps were studied using a BACI design (Smith, 2002; Stewart-Oaten et al., 1986, 1992), a common approach to evaluate restoration effects (Conner et al., 2016; Fisher et al., 2019). The design allows to distinguish impacts by restoration measures from random time variations shared by all sites, as well as from random differences between treatment and control sites (Popescu et al., 2012). We extended the BACI design by using two types of control sites, representing natural and preresoration conditions. In total, we selected three river reaches within the study

area (Figure S1) and inventoried each site in July 2016, 2 years before and in July 2020, 2 years after the restoration.

At the restored site, the riprap was removed (impact) at a cut bank of 500 m in December 2018. Therefore, the soil was sieved to remove the stones and afterwards re-introduced onto the removal site. Before restoration, the cut bank had been stabilized with a riprap since 1989. Directly after riprap removal, the bankfull event in January 2019 caused active erosion with a relocation of the cut bank by 3.3 m on average.

As control sites, we used a natural cut bank that has never been stabilized before (called 'nature control' afterwards) as well as a cut bank that remained stabilized with riprap (called 'stabilized control' or 'riprap' afterwards). At the natural site, active erosion had formed a steep undercut bank (up to 3 m high, 300 m long). At the inventory before restoration, the bank had undergone a period of relatively stable conditions for 3 years. The higher discharge events in February 2017 and January 2019 caused active erosion and a relocation of the cut bank (2017 by 0.8 m, 2019 by 1.8 m) with a restart of succession afterwards. Thus, the successional stages at the natural bank differed between the two inventories from older stages after 3 years of relatively stable, undisturbed conditions in 2016 to recently disturbed early stages in 2020, similar to the restored site in 2020. The stabilized control site (450 m cut bank) was stabilized with porphyry stones since the 1950s. For all sites, we focused only on cut banks (called banks afterwards).

### 2.3 | Vegetation inventory

We selected 14 plots ( $4 \text{ m}^2$ ) at each of the three studied banks, using a stratified random sampling scheme. To cover the heterogeneity within each bank, we randomly selected the vegetation plots within a lower (0–1 m) and an upper (1–2 m) stratum of elevation above mean flow conditions (seven plots per stratum). Depending on the bank inclination, plot form was either  $2 \times 2 \text{ m}$  or  $1 \times 4$  (plot direction parallel to the water line). Within each plot, we identified all vascular plant species and estimated the cover (Braun-Blanquet) of each species in July 2016 and 2020. We used a Differential GPS (R8; Trimble Inc.) to ensure that the re-inventory in 2020 was done at exactly the same plot positions. At the restored and natural sites, where erosion and bank relocation had taken place between both inventories, we re-established the plots at the same elevation and adjusted the position in 2020.

To be able to include two plots without any vegetation at the natural site in 2020 in our analysis, we ascribed species data for these plots with the most frequent species of the natural site in 2020 (*Arrhenatherum elatius*) using the lowest cover class ('r' = one individual, cover = 0.1%). *A. elatius* was present on both plots in 2016. In total, we inventoried 42 vegetation plots (14 plots at three sites) at two points in time (2016, 2020), having 14 replicates (plots) for each time per site.

## 2.4 | Statistical analysis

We analysed differences between natural and stabilized sites as well as the effect of restoration for several dependent variables: vegetation cover, number of species (species richness as measure of alpha diversity) and functional diversity with three indices (functional richness, functional dispersion, functional uniqueness), taxonomic and functional community composition as well as spatial and temporal beta diversity of taxonomic and functional composition (detailed description of variables in Table S2). All variables were calculated at a plot-level basis.

To analyse the functional composition of the communities according to Grime's (1974, 2001) plant strategy theory, we used the CSR strategy information (relative proportion for each C, S and R strategy) from Pierce et al. (2017), available for 85 out of 103 species and calculated community weighted mean (CWM) of every single strategy at each plot. On the basis of the CSR strategy information, we further calculated plot-level functional diversity indices (functional richness, functional dispersion), using the function *dbFD* in package *FD* (Laliberté et al., 2014) as well as functional uniqueness (Ricotta et al., 2016), using the function *uniqueness* provided by Ricotta et al. (2016). For all dependent variables, we applied separate models (called BACI-model afterwards, Table S2) with the same basic structure. In such a BACI model there are two main effects: a Before-After (BA) and a Control-Impact (CI) effect, as well as the interaction term between the BA- and CI-terms ( $BA \times CI$ ; Fisher et al., 2019). The effect of the impact is represented by the  $BA \times CI$ -term, with a significant interaction indicating that the before-after difference at the impact site is significantly different from random or natural time variation at the control sites. To test for the single effects (BA, CI,  $BA \times CI$ ) we used generalized linear models with a stepwise inclusion of effects. Subsequently, Chi-square likelihood ratio tests ( $\chi^2$ ) were applied to assess model improvement and the statistical significance of the explanatory terms (Weisberg & Fox, 2011). We used a quasi-Poisson distribution for species richness (count data) and vegetation cover (cover classes) and a Gaussian distribution for the functional diversity indices (functional richness, functional dispersion and functional uniqueness). For models with a nonsignificant  $BA \times CI$  interaction term (true for vegetation cover, species richness, functional dispersion, functional uniqueness), we extracted differences between natural and stabilized banks as contrast from the model including only the single effects (BA, CI). For models with a significant  $BA \times CI$  interaction term (true for functional richness), we extracted site-site differences (natural vs. stabilized banks) and before-to-after differences for each site with posthoc multiple comparisons (function *glt* in package *multcomp*; Hothorn et al., 2008).

For testing statistical differences in taxonomic and functional composition, we used permutational multivariate analysis of variance (PERMANOVA, Anderson, 2017, function *adonis2* in package *vegan*, Oksanen et al., 2019, and pairwise-PERMANOVA function *pairwise.adonis* in package *pairwiseAdonis*; Martinez Arbizu, 2020) for

posthoc pairwise multiple comparisons, with 5000 permutations and Bonferroni-corrected *p* values of pairwise comparisons. For taxonomic composition, PERMANOVA was based on Bray-Curtis-dissimilarity with species abundances and for functional composition on Marczewski-Steinhaus dissimilarity (Orlóci, 1978, Ricotta et al., 2016) of community weighted mean (CWM) values of CSR strategies. Both dissimilarity indices range from 0 (identical) to 1 (completely distinct).

To quantify spatial and temporal beta diversity of the communities according to Cook et al. (2018), we calculated the multivariate dispersion, using function *betadisper* in package *vegan* (see Table S2 for detailed information). For testing statistical differences in spatial and temporal beta diversity, we used analysis of variance with the BACI-model structure and posthoc Tukey multiple comparison to test for site-site differences (natural vs. stabilized banks) and before-to-after differences for each site.

To identify species that are significantly associated with either natural or stabilized sites or characteristic for early successional stages after restoration, we conducted indicator species analysis using the function *multipatt* in package *indicspecies* (Cáceres & Legendre, 2009) (see Table S2 for detailed information).

All statistical analyses were done with the statistical software R version 4.1.1 (R Core Team, 2020).

## 3 | RESULTS

In total, we found 103 vascular plant species in the inventories before (2016) and after (2020) restoration. The most frequent species was *Arrhenatherum elatius*, followed by *Elymus repens* and *Rubus caesius*. We found two species of conservation concern: *Epilobium obscurum* (critically endangered) and *Sisymbrium strictissimum* (considered regionally extinct according to Red List of Saxony-Anhalt 2020, Frank et al. 2020).

### 3.1 | Comparing natural and stabilized riverbanks

Compared to the stabilized banks, the natural bank showed a significantly lower vegetation cover (sparse and patchy) with a significantly lower number of species, especially after disturbance by flooding in 2019 (Table 1).

Species composition at the natural bank was significantly different from the stabilized bank (Table 2 and Figure 1; mean Bray-Curtis-dissimilarity natural vs. riprap = 0.87, pairwise adonis pseudo-*F* = 5.86, *p* < 0.01, *R*<sup>2</sup> = 0.10). Indicator species analysis identified three species that are characteristic for the natural bank (*Trifolium arvense* in 2016, *Xanthium strumarium* and *Senecio viscosus* in 2020, Table S1). We did not find species that are jointly characteristic for both points in time at the natural site. Six species are characteristic for stabilized banks in general (*Elymus repens*, *Arrhenatherum elatius*, *Dactylis glomerata*, *Rumex acetosa*, *Rubus caesius*, *Bromus inermis*). Besides these general indicator species for

**TABLE 1** Summary statistics of different facets of vegetation diversity at restored, natural and stabilized (riprap) banks before (2016) and after restoration (2020)

Bank type	Time	Vegetation cover (%)	Species richness	Functional richness	Functional dispersion	Functional uniqueness
Restored	Before	55 (17)	10.1 (6–13)	5.25 (1.59)	1.06 (0.32)	0.43 (0.10)
Restored	After	37 (21)	15.7 (2–33)	10.11 (2.99)***	1.15 (0.47)	0.51 (0.11)
Natural	Before	30 (19) <sup>a</sup>	8.8 (6–14) <sup>a</sup>	5.12 (2.58) <sup>a</sup>	0.87 (0.28)	0.37 (0.09)
Natural	After	19 (25)	7.4 (1–20)	5.00 (3.62)	0.70 (0.69)	0.46 (0.15)
Riprap	Before	64 (10) <sup>b</sup>	9.4 (6–13) <sup>b</sup>	6.57 (2.91) <sup>b</sup>	0.94 (0.30)	0.41 (0.09)
Riprap	After	50 (24)	13.3 (10–20)	8.47 (2.75)	0.97 (0.35)	0.43 (0.05)

Note: Mean (SD) for vegetation cover, species richness (min-max instead of SD), functional richness, functional dispersion and functional uniqueness. For each facet, mean differences between natural and stabilized banks irrespective of time are marked with small letters ( $p < 0.05$ ). For facets without letters, no differences between natural and stabilized banks were observed. Significant differences between before and after for each site are marked according to \*\*\* $p < 0.001$ .

**TABLE 2** Summary of BACI-models to test for effects of restoration as well as differences between natural and stabilized (riprap) banks

	Dependent variables											
	Dissimilarity of species composition			Dissimilarity of functional composition (CSR strategy)			Spatial beta diversity			Temporal beta diversity		
	pseudo-F	R <sup>2</sup>	p	pseudo-F	R <sup>2</sup>	p	df	F	p	df	F	p
Comparison of natural and stabilized banks												
								Difference*	p*	Difference*	p*	
Natural–riprap	5.86	0.10	**	19.49	0.27	**		0.06	*	0.08	***	
Effect of restoration												
Before–After (BA)	9.23	0.09	***	1.06	0.01	ns	1	35.22	***	1	39.60	***
Control–Impact (CI)	5.78	0.11	***	11.11	0.21	***	2	5.10	**	2	9.20	***
BA × CI	3.24	0.06	***	2.55	0.05	*	2	8.72	***	2	9.91	***
BA restored	9.16	0.26	*	1.40	0.06	ns		0.12	**		0.10	**
BA natural	3.89	0.13	*	3.33	0.11	ns		0.20	***		0.17	***
BA riprap	3.07	0.11	ns	0.59	0.02	ns		0.01	ns		0.01	ns

Note: For dissimilarity of species composition and functional composition, we used permutational multivariate analysis of variance (PERMANOVA) and posthoc pairwise-PERMANOVA for site-site comparisons of natural and stabilized banks as well as before-after comparisons of single sites. For spatial and temporal beta diversity of species composition, we used analysis of variance and posthoc Tukey tests for site-site as well as before-after comparisons. For Tukey tests group differences and  $p$  values are shown (fields marked in grey and with\*). CSR, competitor, stress tolerator, and ruderal; ns, nonsignificant difference. Bonferroni-corrected  $p$  values of all pairwise comparisons are shown \* $p < 0.05$ ; \*\* $p < 0.01$ ; \*\*\* $p < 0.001$ .

riprap banks, we found several species with significant association to the individual riprap sites at single points in time (Table S1).

Spatial beta diversity of species composition was significantly higher at the natural bank compared to the stabilized bank (Table 2 and Figure 2). At the natural bank we observed a significant temporal turnover of species composition between years (caused by the flood in 2019) but not so in the stabilized bank (Table 2 and Figure 2).

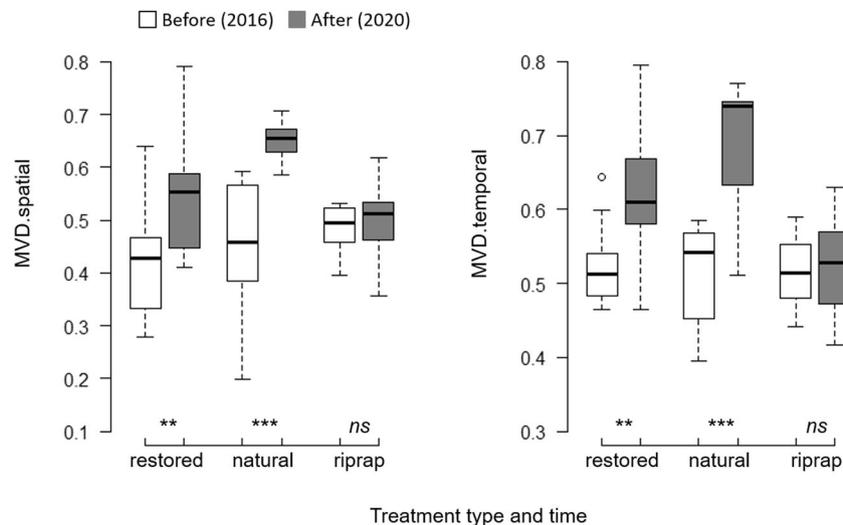
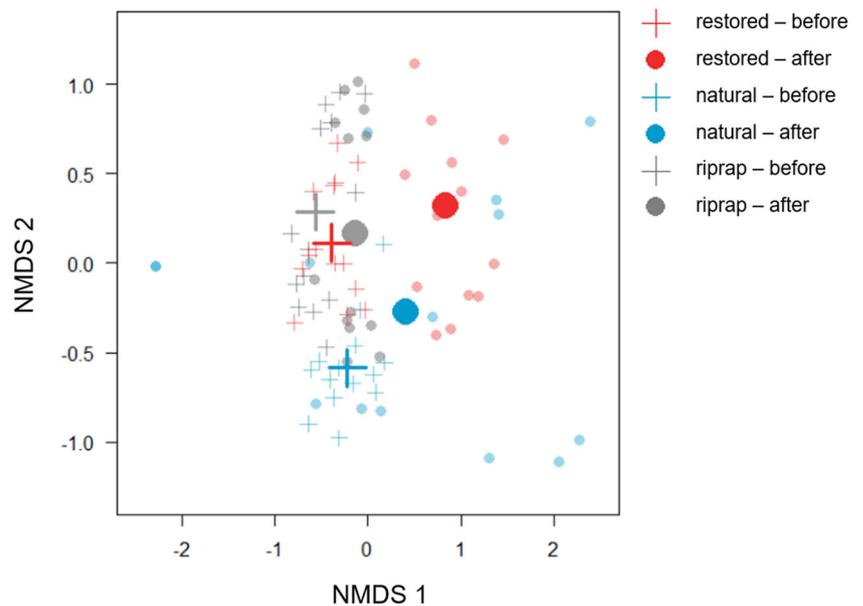
Functional composition of the natural bank is significantly different from the stabilized bank (Table 2 and Figure 3). At the natural bank the competitor-CWM is significantly lower (natural = 23.2%, riprap = 37.4%,  $p < 0.001$ , Tukey multiple comparison) and the stress-tolerant-CWM significantly higher (natural = 36.3%, riprap = 26.3%,  $p < 0.01$ ) compared to the stabilized bank. The ruderal-CWM is not different between the natural and the stabilized bank

(natural = 40.5%, riprap = 36.3%). The community at the natural bank shows a significantly lower functional richness compared to the stabilized bank (natural = 5.1, riprap = 7.5,  $p < 0.05$ ). Functional dispersion and functional uniqueness were not significantly different between bank types (Table 1). Spatial and temporal beta diversity of functional composition were not different between the sites.

### 3.2 | Effects of restoration

The removal of bank fixation had a significant effect on species composition (Table 2 and Figure 1) as well as on the spatial and temporal beta diversity of species composition (Table 2 and Figure 2).

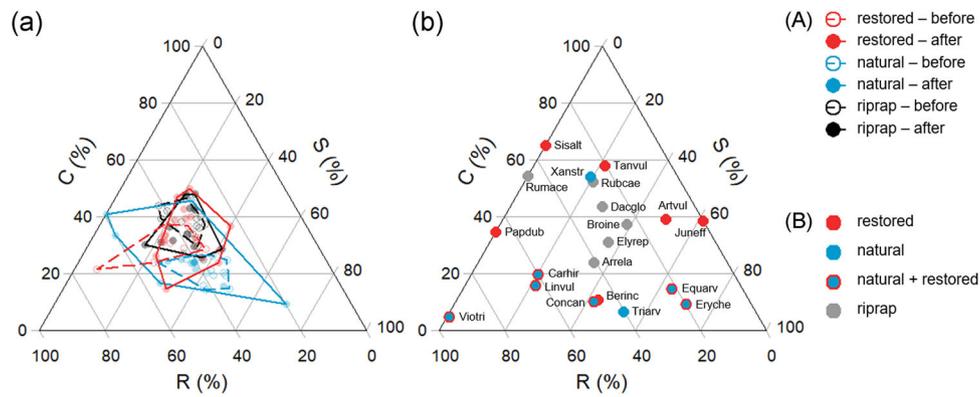
**FIGURE 1** Two-dimensional NMDS showing species composition of the 42 vegetation plots (species abundance data, Bray-Curtis-dissimilarity) at restored, natural and stabilized (riprap) banks before (2016) and after restoration (2020) (stress = 0.15, three dimensions). Large symbols show centroids of groups and small transparent symbols show single plots



**FIGURE 2** Spatial (left) and temporal beta diversity (right) of species composition for restored, natural and stabilized (riprap) banks before (2016) and after restoration (2020). Spatial beta diversity is measured as multivariate dispersion (MVD) of plots around sampling event centroids. Temporal beta diversity is measured as the difference in multivariate dispersion of plots around site centroids between before (2016) and after restoration (2020). A significant difference between before (2016) and after restoration (2020) can be interpreted as a significant temporal community turnover at a site between both points in time. ns, nonsignificant difference. Statistical significance of differences between before and after restoration is given: \* $p < 0.05$ ; \*\* $p < 0.01$ ; \*\*\* $p < 0.001$

Species composition significantly changed from before to after the restoration at the restored site (mean Bray-Curtis dissimilarity BS-dist = 0.89) and at the natural site (BC-dist = 0.86) but not at the stabilized site (riprap, BC-dist = 0.53; significant interaction BA  $\times$  Cl, Table 2 and Figure 1). At the restored bank this change in species composition was mainly caused by gaining species after the restoration that have not been present before (57% of total site species pool). A small proportion of species (25%) remained from before the restoration. In contrast, at the control banks, a much larger proportion of species persisted between the years (nature: 47%, riprap: 47%) and a smaller proportion was gained (nature: 29%,

riprap: 44%). The fraction of species that were lost between the years was comparably low at all sites (restored: 18%, nature: 24%, riprap: 9%). The majority of species that were gained after restoration are exclusive to the restored site (29 species gained in total, 17 new to the system after restoration, 12 present in the system before the restoration; Table S3). The ruderal strategy of these newly gained species was higher compared to the whole-community ruderal strategy before the restoration (45.4% gained species, 41.2% all species before). The majority of gained species at the restored bank possess a binary CR strategy type. The same was observed at the natural bank that experienced a significant species turnover after the



**FIGURE 3** (a) Functional composition (abundance-weighted mean competitor, stress tolerator, and ruderal [CSR] strategy) of communities of the 42 vegetation plots at restored, natural and stabilized (riprap) banks before (2016) and after restoration (2020), showing the convex hulls for the different bank types before and after restoration. (b) CSR strategy of species with significant association to the different bank types (restored, natural, stabilized). For stabilized (riprap) banks the general indicator species are shown, that are significantly associated with more than one individual riprap site. Species: *Arrhenatherum elatius* (Arrela), *Artemisia vulgaris* (Artvul), *Berteroa incana* (Berinc), *Bromus inermis* (Broine), *Coryza canadensis* (Concan), *Carex hirta* (Carhir), *Dactylus glomerata* (Dacglo), *Elymus repens* (Elyrep), *Equisetum arvense* (Equarv), *Erysimum cheiranthoides* (Eryche), *Glechoma hederacea* (Glehed), *Juncus effusus* (Juneff), *Linaria vulgaris* (Linvul), *Lotus corniculatus* (Lotcor), *Papaver dubium* (Papdub), *Rubus caesius* (Rubcae), *Rumex acetosa* (Rumace), *Sisymbrium altissimum* (Sisalt), *Tanacetum vulgare* (Tanvul), *Trifolium arvense* (Triarv), *Viola tricolor* (Viotri), *Xanthium strumarium* (Xanstr)

bankfull events (ruderal strategy of gained species 43.1%, 40.5% all before). Additionally, stress-tolerant strategy of gained species after disturbance was lower compared to the whole-community stress-tolerant strategy before at the natural bank (21.7% gained species, 29.6% all before).

We found seven species with significant association to the early recolonization stage after the removal of riprap (*Tanacetum vulgare*, *Artemisia vulgaris*, *Sisymbrium altissimum*, *Juncus effusus*, *Papaver dubium*, *Berteroa incana*, *Populus specimen*). Further, we found three species with significant association to both the natural and the restored bank in 2020 (*Viola tricolor*, *Linaria vulgaris*, *Erysimum cheiranthoides*) and three species (*Carex hirta*, *Equisetum arvense*, *Coryza canadensis*) for the restored bank and the natural bank in both years (Table S1).

Spatial beta diversity and temporal turnover of species composition significantly increased after restoration, similar to the increase observed at the natural bank and in contrast to no changes at both nonrestored stabilized banks (significant interaction BA × CI, Table 2 and Figure 2).

Functional richness of the community increased significantly after restoration, in contrast to all other sites (significant interaction BA × CI, Table 1), while the functional composition and spatial heterogeneity of functional composition, functional dispersion and functional uniqueness were not significantly changed due to restoration (Table 1 and Table 2).

## 4 | DISCUSSION

We investigated the early effects of restoration by removal of riprap and compared the results with two types of control sites, representing natural and pre-restoration conditions. Most importantly, our

results showed that spatial heterogeneity and temporal turnover of species composition significantly increased at the restored bank, similar to the increase observed at the natural bank and in contrast to no changes at the nonrestored stabilized banks, which is in line with our hypothesis 1. Species composition was significantly different after restoration, mainly because of gaining species from the local species pool that have not been present before. Contrary to our expectation, this change in species composition was not inducing a change in functional composition (hypothesis 2). Functional composition after the restoration remained similar to the pre-restoration condition and we did not observe an increase of ruderals as expected after the disturbance caused by the restoration and subsequent natural dynamics (Göthe et al., 2016, Modrak et al., 2017). Likewise, differences in functional composition between the natural and stabilized control reaches were unexpected, as we did not observe a higher proportion of ruderals at the natural bank. Functional richness significantly increased after restoration, as expected, but functional dispersion and functional uniqueness remained unaffected, in contrast to our expectations (hypothesis 3). Natural and stabilized control reaches did not differ in functional diversity (richness, dispersion, uniqueness), contrary to hypothesis 3.

### 4.1 | Re-establishment of heterogeneity

A high spatiotemporal heterogeneity is a typical feature of riverbanks at their natural state caused by frequent disturbances (Naiman & Décamps, 1997), as observed at the natural control site at the River Mulde. The removal of riprap enabled the re-establishment of such dynamic processes (erosion, sedimentation) at the restored site as indicated by an increased spatial heterogeneity and temporal

turnover of the vegetation community. The bankfull discharge event that happened shortly after the restoration increased the physical complexity at the restored bank by creating a heterogeneous mosaic of site conditions (different bank inclinations and substrate grain sizes). We propose, that the increased habitat heterogeneity was accompanied by an increased heterogeneity of the recolonizing vegetation, similar to the natural site and in contrast to the stabilized control sites. A re-established higher disturbance level and increased heterogeneity of both abiotic environment and vegetation improves habitat conditions for many other specialized and low-competitive species of various organism groups that depend on open patchy sites with bare sediment such as ground beetles (Januschke & Verdonschot, 2016; Sprößig et al., 2020). The cross-ecosystem study from Pilotto et al. (2019) revealed that several taxonomic groups, including vegetation, benefitted from an increased physical complexity following restoration in both the river channel and the floodplain area. However, restoration of degraded environments has not always succeeded in enhancing biodiversity via an increase of physical habitat heterogeneity (Palmer et al., 2010), mainly due to the overriding effects of remaining stressors (altered flow regimes, dispersal barriers) that prevent species recolonization.

Even under the huge disturbance that was caused by the removal of riprap in our study, the observed increase in spatial heterogeneity and temporal turnover of the vegetation was still smaller at the restored site compared to the changes at the natural site after the bankfull event. This is probably due to the remaining larger stones and compacted soil after the removal of riprap that hampered erosion. One single (minor) bankfull event may not be sufficient to fully re-establish erosion and sediment translocation compared to the natural bank.

Further, we interpret the small number and the changing identity of indicator species (no shared indicator species between the years) at the natural and restored sites as indicators for dynamic processes that cause disturbances and distinct shifts in community composition between years. In contrast, at stabilized sites, we found numerous indicator species that were shared by sites and years. This pattern was also observed by Wollny et al. (2019) at the Danube River and the Main River. Given a lack of indicator species in dynamic habitats a trait-based approach might be more suitable for characterizing vegetation change in floodplain restoration. The usefulness of functional traits to analyse responses to restoration has already been shown in several studies (Fournier et al., 2015; Göthe et al., 2016; Modrak et al., 2017; Muhar et al., 2016). Although the trait-based approach has shown weaker responses to restoration than the taxonomic-based approach in some studies (Januschke et al., 2011; Pilotto et al., 2019) it provides mechanistic insights into the drivers of community changes following restoration.

## 4.2 | Community composition

A significant turnover in community composition after removal of riprap is expected (reported by Göthe et al., 2016; Modrak et al., 2017)

because of profound alterations of abiotic habitat conditions. In addition to other studies that analyse the distinctiveness of the community after restoration from the preresoration condition, the natural control site in our study allows to compare the process of recolonization at the restored and the natural bank after disturbance (both recently disturbed by bankfull discharge event in 2020, both early successional stages). Plants can recolonize sites after floods or restoration via different mechanisms: by germination from the seedbank, resprouting from vegetative organs that remained in the soil, by receiving plant propagules or seeds that are transported with the river water (hydrochorous, nautochorous species) or anemochorous seed dispersal (Cavallé et al., 2015; Hasselquist et al., 2015; Nilsson et al., 2010). Especially by the latter dispersal processes, species pass a dispersal filter (Fraaije et al., 2015) that shapes community composition after restoration/disturbance and species possessing particular traits will be favoured.

Specifically, hydrochorous species (Hasselquist et al., 2015) and particularly species with ruderal traits (short life cycles, large seed production) may be favoured by an increased availability of open patches after restoration or flooding events (Göthe et al., 2016). Contrary to our expectation, the observed taxonomic responses were stronger than those of traits, as the changes in taxonomic composition did not translate into changes in functional composition. However, even though we have not observed a significant change in the CSR strategy at the community level after restoration, the newly established species at the restored bank that were not present before, showed a distinct CSR strategy compared to all species present before restoration. The ruderal strategy of these newly gained species was higher compared to the whole-community ruderal strategy before the restoration, similar to the natural site. Additionally, stress-tolerant strategy of gained species after the disturbance was lower compared to the whole-community stress-tolerant strategy before at the natural bank. Similar to Cavallé et al. (2015), the majority of gained species reached the restored bank via seed dispersal by different vectors (wind, water, animals), whereby many wind-dispersed species are also successfully dispersed by water during floods because they also have the ability to float (Johansson et al., 1996). Among them were annual ruderal species that were significantly associated with the early successional stage at the natural bank or after restoration (*Erysimum cheiranthoides* [CR], *Viola tricolor* [R], *Xanthium strumarium* [CR]; CSR strategy in brackets). In contrast, species that persisted between the years at both restored and natural bank were predominantly longer-living (pluriennial pollakanthic) by the ability to resprout from vegetative organs and possessing a competitor-strategy type. These persistent species, often high in abundance, shape the community level CSR strategy and overwrite changes in functional community composition after restoration or natural disturbance, especially if species turnover is low. Distinct shifts in diversity and abundance of plant growth forms and plant life strategies, especially an increase in short-lived ruderals and a decline in stress-tolerant species following restoration, were observed by Poulin et al. (2013), Göthe et al. (2016) and Modrak et al. (2017). This is in line with findings from a meta-analysis

(Pilotto et al., 2019), showing that overall trait diversity was higher at restored than at control reaches. Similarly, at the Mulde River, the functional richness of CSR strategies was significantly higher after restoration, while functional dispersion and functional uniqueness were unaffected. As the natural and the stabilized riverbanks did not differ in any of the functional diversity indices, we interpret the increased functional richness after restoration as an immediate effect of the disturbance itself and expect that functional richness will decrease and become similar to the natural bank given time.

The early changes, 2 years after restoration, indicate that a substantial proportion of the community, especially the gained species, became more similar to the natural bank community. Such early changes are shaped by short-distance dispersal of species from the local species pool, while an increase of species that indicate regular flooding, like observed by Modrak et al. (2017) is expected to happen in the longer term. This is due to a time lag between restoration and recolonization, that depends on factors such as dispersal abilities and distance to source populations (Huxel & Hastings, 1999). However, even at the natural bank, communities are dominated by common species without a strong association to floodplain habitats. Species that are indicative for riverbanks in a natural state are rare in the local upstream species pool, but they frequently occur downstream the investigated reaches on gravel banks and slip-off slopes. However, we only find a few of these structures upstream, because the majority of upstream riverbanks are stabilized. Additionally, the whole system's hydrological regime is influenced by the reservoir upstream reduces the magnitude and the frequency of water level changes. Thus, receiving plant propagules from potential source habitats is limited and depends on rare events of long-distance propagule transport. In a meta-analysis of several restoration projects, Göthe et al. (2016) did not find evidence for an increased abundance or diversity of hydrochorous species in response to restoration. This was unexpected, because hydrochorous species may be among the first to establish following restoration (Hasselquist et al., 2015; Nilsson et al., 2010). However, hydrochory is greatly affected by instream barriers such as dams and weirs as they disrupt the natural hydrologic regime and the longitudinal connectivity within stream networks (Nilsson et al., 2010). This is also true for the study area at the Mulde River that is affected by upstream barriers, which may have contributed to the weak response of hydrochorous species following restoration. Additionally, we might have underestimated the occurrence of hydrochorous species as propagules are more likely to settle near the waterline and we have not explicitly sampled this area. Especially, the water level at the inventory after restoration was much lower following the extreme drought and thus the predefined plot locations from the inventory before restoration has no longer covered this important stratum directly influenced by the river water level.

### 4.3 | Differences between natural and stabilized riverbanks

From our knowledge presented in the literature, natural riverbanks as dynamic and resource-poor habitats, show a different diversity and

distinct taxonomic and functional community composition compared to stabilized riverbanks (Wollny et al., 2019 and references therein). At the Mulde River, the observed differences were partly unexpected, as we did not observe a significantly higher proportion of ruderals at the natural bank. Furthermore, plot-level functional richness was significantly lower at the natural bank compared to the stabilized site, while functional dispersion and uniqueness did not differ between the bank types. Most likely, the significantly lower functional richness at the natural site can be explained by its low species richness, as species richness and functional richness are correlated (Cadotte et al., 2011). Even if the Mulde River is one of the most near-natural lowland rivers in Germany, unmodified reaches are rare, as about 75% of the riverbanks are stabilized by riprap (Puhmann, 1997). Likewise, along German national waterways, the majority of riverbanks are stabilized and frequently disturbed, open sites became rare at the landscape scale, thus explaining an overall rareness of ruderals and underlining the ecological extent of these alterations (Wollny et al., 2019). In line with theory, we observed a higher CWM of stress-tolerant strategy at natural banks. Stress-tolerant species show resilience towards environmental stressors such as flooding and are further promoted by delayed growth of more competitive species by, for example, regular flooding (Baatrup-Pedersen et al., 2013). These authors point out that stress tolerance may indicate flooding, whereas ruderals indicate erosion and sedimentation and thus higher river dynamics. In contrast, the stabilized riverbanks are dominated by late-successional species from mesic grassland floodplain meadows possessing a competitor strategy type, like observed by Wollny et al. (2019). Thus, community dynamics at natural banks are rather controlled by disturbances causing abiotic spatiotemporal habitat heterogeneity while in contrast, under stabilized settings, community dynamics are controlled by competition rather than disturbances (Wollny et al., 2019). Likewise, the low proportion of specialized and functionally differentiated species at the natural bank might explain that we have not observed a significantly higher functional diversity at the natural site. Nevertheless, we observed the tendency to a higher spatial and temporal heterogeneity (beta diversity) of functional composition at the natural bank and following restoration, as indicated by the larger convex hulls and higher dispersion of plots (Figure 3).

Even if plot-level taxonomic diversity (alpha diversity) is lower at natural unmodified reaches compared to stabilized ones, the spatio-temporal beta diversity is much higher at natural reaches. Additionally, at a larger spatial scale, natural reaches show a higher beta diversity of morphological structures with distinct vegetation types (cut banks, slip-off slopes, and gravel banks) and wider transition zones between aquatic and terrestrial habitats (Bunn & Arthington, 2002). In contrast, stabilized reaches are very uniform with steep abiotic gradients.

## 5 | CONCLUSION

Including a natural control site allows for a better interpretation of restoration effects, as they allow to compare changes after restoration to natural dynamics and to distinguish from impact-related alterations

resulting from the restoration itself. On that basis, our findings show most importantly, an increased spatiotemporal heterogeneity of the vegetation after removal of riprap, being an indicator for re-established dynamic processes similar to the natural site. The early changes in vegetation composition 2 years after restoration indicate, that a substantial proportion of the community, especially the newly established species, became more similar to the natural bank community. Specifically, ruderal species, that are related to frequently disturbed sites, established in the first year after restoration. At the same time, very competitive species from before the restoration persisted at the site by vegetative resprouting. Thus, the long-term succession at the restored site is highly dependent on the future disturbance frequency, especially during periods with low discharge due to climatic extremes. As dispersal and retention of propagules depend on high-discharge events, they are of overriding importance for species establishment in restored sites and for resetting succession. This highlights the importance of long-term monitoring of the restored and control sites to evaluate restoration effects. Creating open patchy habitat conditions and delaying the growth of competitive persistent species are prerequisites for specialized, low-competitive species. Such habitats are rare along regulated rivers but important refugia and source habitats for future restoration sites.

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## AUTHOR CONTRIBUTIONS

Carolin Seele-Dilbat, Lena Kretz and Christian Wirth conceptualized the study. Carolin Seele-Dilbat and Lena Kretz conducted fieldwork and gathered vegetation data. Carolin Seele-Dilbat analysed the data and interpreted the results. All authors contributed to writing the manuscript.

## ORCID

Lena Kretz  <http://orcid.org/0000-0002-8040-4421>

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