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Continuous riverine biodiversity changes in a 10-years-postrestoration-study—Impacts and pitfalls

Armin W. Lorenz 💿

Faculty of Biology, Department of Aquatic Ecology, University of Duisburg-Essen, Essen, Germany

Correspondence

Armin W. Lorenz, Faculty of Biology, Department of Aquatic Ecology, Universitätsstr. 5, 45117 Essen, Germany. Email: armin.lorenz@uni-essen.de

Abstract

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Evaluating river restoration effects over several years is the exception rather than the rule. The benthic invertebrate fauna of three small mountain streams was investigated yearly from 2010 to 2019 following remeandering measures. Additionally, upstream near-natural reaches were studied following a Before-After-Control-Impact (BACI) design. Species richness and Ephemeroptera, Plecoptera and Trichoptera richness decreased strongly immediately after restoration but had positive effect sizes in the following 6 years. Abundances increased in all sites after restoration. These patterns were consistent also in the upstream near-natural reaches, except for the decrease in richness in the second year, indicating that other factors beside the restoration affected the sites. A large flood event coincided with the implementation of the restoration measures depleting also the near-natural sites. The similarity between paired reaches showed a sharp decline in the first year after restoration, followed by a direct increase, which indicates fast recolonization from the upstream reaches. Community composition analysis showed a shift of all communities with the time axis, underlining a substantial effect of external factors. Generalized linear mixed effects models exhibited that the percentage of tree cover and riparian vegetation had significant effects on changes in richness and abundance. Clear-cut logging in the floodplains to restore natural floodplain forest supposedly increased water temperatures because many cold-adapted upstream species were replaced by species naturally inhabiting more downstream reaches. The results emphasize that multiannual samples and a BACI design are necessary to understand restored systems. Furthermore, floodplain restoration and natural hydrology often shape benthic invertebrate communities more than pure instream restoration measures.

KEYWORDS

benthic invertebrates, droughts, floodplain restoration, longitudinal preferences, stream restoration, water temperature

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1 | INTRODUCTION

River restoration is a hot topic in the recent two decades (Beechie, Pess, & Roni, 2008; Palmer et al., 2005) and the number of studies on the effects of river restoration measures is strongly increasing (Feld et al., 2011). There is a large diversity in effect studies covering time scales, biotic groups or morphological changes. Most frequently, short-term effects are investigated, targeting effects within the first 2-5 years after restoration (e.g., Howson, Robson, & Mitchell, 2009; Nilsson et al., 2015; Tikkanen, Laasonen, Muotka, Huhta, & Kuusela, 1994). Longer time scales of 10-20 years after restoration are rare (but see Muotka, Paavola, Haapala, Novikmec, & Laasonen, 2002; Louhi et al., 2011). This problem is inherent to the relatively new research topic. Furthermore, besides the relatively short time between restoration and investigation, most studies investigate only 1 or 2 years or seasons. Thus, long-term data sets are largely missing, that is, studies of restoration effects for a time span of more than 5 or 10 years (but see Friberg, Kronvang, Hansen, & Svendsen, 1998 and Louhi et al., 2011). To overcome this shortcoming, several authors focused on meta-analyses with data sets of different restoration measures and different time frames after restoration (Kail, Brabec, Poppe, & Januschke, 2015; Lorenz, Haase, Januschke, Sundermann, & Hering, 2018; Miller, Budy, & Schmidt, 2010). Nonetheless, these do not account for interannual variation, the stability of biotic communities and the inherent succession (Dyste & Valett, 2019).

Fish and benthic invertebrates are the most frequently studied response organism groups. For both taxonomic groups the overall impression is that the list of investigations is long but the list of really observed biotic improvement is very short (Feld et al., 2011; Louhi et al., 2011: Nilsson et al., 2015). Nonetheless, there is a bias in the underlying datasets. Mostly, restoration measures are implemented in short sections of vastly degraded river systems. Thus, the expectation of an improving community might be unrealistic (Parkyn & Smith, 2011), as the chance of sensitive species reaching restored sections is low, not to mention their establishment. Furthermore they often need continuously good water quality (Sundermann, Gerhardt, Kappes, & Haase, 2013) and specific habitats (Pilotto, Bertoncin, Harvey, Wharton, & Pusch, 2014). Thus, the question remains, how does biology react if a restoration measure is implemented in a river system, which is only under minor anthropogenic pressure or in a system where near-natural morphology is the standard and degraded sections are the exception? Dispersal constraints or missing species pools (Sundermann, Stoll, & Haase, 2011) are not a limiting factor, which might probably lead to a fast recolonization by sensitive species from upstream and downstream sections.

Morphological restoration comprises many different targets and techniques. The removal of a large dam can be seen as the one end of the gradient, and abandoning management of the river banks, a passive restoration measure, as the other end. Effects of those measures are for sure different, manifest within greatly different time intervals and act differently on biological groups. Besides the longitudinal aspects of, for example, dam removal, remeandering measures or improvement of instream habitats, the lateral aspect, that is, floodplain restoration, is often overlooked. Floodplain restoration clearly affects riparian vegetation composition and structure (Göthe, Timmermann, Januschke, & Baattrup-Pedersen, 2016; Modrak, Brunzel, & Lorenz, 2017) and might also affect aquatic communities, as differing forms of landuse have substantial effects on aquatic communities (Quinn, Cooper, Davies-Colley, Rutherford, & Williamson, 1997). Not only the agricultural or urban impact needs to be considered here, but also clear-cutting in forested catchments (Noel, Martin, & Federer, 1986). If those general landuse changes detrimentally influence benthic invertebrate communities then floodplain restoration which is a form of landuse change might also have a substantial impact.

A key factor influencing the distribution of benthic invertebrates in river systems is water temperature (Caissie, 2006). Illies and Botosaneanu (1963) developed the Rhithral-Potamal concept mainly based on longitudinal changes of water temperature parameters. For central European benthic invertebrate species the longitudinal preferences are well known and summarized in an online platform (Schmidt-Kloiber & Hering, 2015). But water temperatures increase unnaturally when floodplain vegetation is altered, for example, by changes to agricultural area or by clear-cutting (Brown & Krygier, 1970). Thus, the instream communities might be affected by restoration measures conducted in the floodplain.

This double influence of longitudinal restoration, that is, morphological restoration in the river bed and lateral restoration, that is, floodplain restoration is rarely considered.

The Arnsberg forest is a large forested area in Western Germany. Morphology of most of the streams is near-natural and only short sections have been previously straightened. Pre-restoration evaluation of the invertebrate communities displayed an overall good ecological status of the catchments. Nonetheless, funded by an EU-life project (www.life-bachtaeler.de), the remaining straightened sections were restored and a general change in the floodplains was initiated from non-native coniferous trees to indigenous deciduous trees. This gave the chance to investigate restoration measures in a more natural surrounding. Benthic invertebrate community patterns were investigated continuously at three sites starting before the restoration measures in the year 2010 until 2019 (1 year before; 10 years of sampling in total). Besides the restored sites upstream near-natural sites were sampled allowing for a Before-After-Control-Impact (BACI) design in the analysis. The objectives of the study are to shed light on short- and longterm effects of restoration measures in a more natural environment comparing the influence of instream and floodplain restoration. The following questions will be answered: How do the benthic invertebrate communities respond to the morphological changes over the time span of 10 years? And, how do the benthic invertebrate communities respond to the landuse changes in the floodplain?

2 | MATERIAL AND METHODS

Three small mountain streams were investigated in the Arnsberg Forest in the western central part of Germany (Table 1). Catchment sizes

| TABLE 1 | Characteristics of the | six sampling sites | | | | | | | |
|---------|------------------------|--------------------|-------------------------|------------------------|--------------|-----------|-------------------------|--------------------------------|-----------------------------------|
| Site | Status | Stream | Catchment size (km²) | Altitude (m a.s.l.) | Slope (%) | H | Conductivity (μS/cm) | O ₂ -saturation (%) | O ₂ -content (mg/L) |
| KS-nat | Near-natural | Kleine Schmalenau | 4.5 | 292 | 0.83 | 7.8 ± 0.7 | 114 ± 7 | 82.1 ± 17.4 | 10.4 ± 0.9 |
| KS-res | Restored | Kleine Schmalenau | 4.8 | 290 | 0.67 | 7.5 ± 0.7 | 122 ± 12 | 94.8 ± 11.8 | 10.8 ± 0.9 |
| GS-nat | Near-natural | Große Schmalenau | 16.9 | 258 | 0.95 | 7.6 ± 0.5 | 107 ± 13 | 93.1 ± 9.0 | 10.9 ± 1.5 |
| GS-res | Restored | Große Schmalenau | 18.3 | 245 | 0.87 | 7.5 ± 0.6 | 101 ± 4 | 102.5 ± 20.6 | 11.4 ± 1.7 |
| H-nat | Near-natural | Heve | 46.3 | 252 | 0.40 | 7.1 ± 0.6 | 132 ± 9 | 108.6 ± 20.3 | 10.3 ± 1.0 |
| H-res | Restored | Heve | 47.1 | 246 | 0.40 | 7.3 ± 0.5 | 132 ± 10 | 91.1 ± 11.5 | 10.2 ± 0.9 |
| | | | | | | | | | |

ranged between 5 km² (Kleine Schmalenau) and 47 km² (Heve), with catchments being dominated by coniferous forest with urban settlements and agriculture almost completely lacking. Forests are dominated by spruce (*Picea abies*), which is not native in this region. The geology is schist (siliceous) and the streams' substrate is cobble-dominated with minor percentages of sand, woody debris and macrophyte patches. Mean annual rainfall for the area is 900 L/m² and mean annual temperature is 8.4°C. The streams are naturally perennial though may be partly reduced in extraordinary hot and dry summers to disconnected pools due to ceased run-off. The last time this was observed in summer 2003.

In the winter 2010/2011, short straightened sections of the streams Heve and Kleine Schmalenau were restored. In winter 2012, an additional restoration was conducted in the Große Schmalenau. Restoration measures included the digging of new meandering water-courses. The straightened channels were clogged with earth's lumps. The restoration measures were conducted in the course of an EU-funded life-project ("Bachtäler im Arnsberger Wald"; project time scale 2009–2014). A second goal of the life-project was to change the floodplain vegetation from non-native spruce to native elder communities. Hence, over the 5-year-period of the project, logging and reforestation was conducted patchily in many parts of the project area.

The study started in 2010 before the restoration measures were conducted and followed a BACI design. In the Kleine Schmalenau and the Große Schmalenau, one degraded site and one near-natural site were sampled: the near-natural sites were located 200 m and 1 km upstream of the degraded sites, respectively. In the Heve only a degraded site was sampled. From 2010 to 2019 both sites of the Kleine Schmalenau and the restored site of the Heve were sampled every year. The degraded site of the Große Schmalenau was sampled in 2010 and starting after the restoration (winter 2012) from 2013 until 2019. In the first years the near-natural sites of the Heve and of the Große Schmalenau were sampled irregularly. The site in the Große Schmalenau was not sampled in 2011, 2015 and 2017. The nearnatural site in the Heve was not sampled in 2010, 2013, 2016 and 2018. Invertebrate samples were taken around the 10th of April each year. A standardized multi-habitat-sampling was conducted (Meier et al., 2006) by taking 20 subsamples (shovel sampler: 25×25 cm, 500 µm mesh size) concordant to the distribution of substrates present at each site. The substrate distribution was recorded in 5% steps. The sites' subsamples were pooled, conserved with 90% ethanol and transported to the lab for sorting. In the lab, a standardized subsampling procedure was applied (Meier et al., 2006). The specimens were identified to the lowest level possible, mainly species and genus with the exception of Chironomidae (tribe level) and Oligochaeta (family level), according to the operational taxa list for Germany (Haase et al., 2004) (Table S1).

On-site pH, conductivity and oxygen were measured for background information.

A gauge station is operating downstream the confluence of the Große Schmalenau and the Heve. The restored sites of the Große Schmalenau and the Heve are located 300 m and 1 km upstream, respectively. The Ruhrverband provided the gauging data of the last 20 years for analysis.

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ASTERICS, the official assessment tool for the implementation of the EU-water framework directive (WFD) in Germany (downloadable at: www.fliessgewaesserbewertung.de), was used to calculate metrics and trait percentages for the taxa lists resulting from the pooled samples.

Species richness, abundance (per m²) and Ephemeroptera, Plecoptera and Trichoptera (EPT) richness served as main explanatory metrics. For each post-restoration sample and each metric an effect size was calculated to value the changes induced by the restoration measures. The effect size was calculated as metric value after the restoration minus the respective metric value before the realization of the restoration measures. For comparison the same calculation was conducted on the samples of the control sites, that is, the near-natural sites. Thus, the calculations followed a BACI design. The results were tested with the Wilcoxon test.

Furthermore, the analysis focused on metrics concerning the longitudinal preferences of invertebrate species (Moog, 1995) which reflect temperature regimes of river sections. The different longitudinal categories are defined as: epirhithral (small mountain brooks, thus the upper trout region), metarhithral (lower trout region), hyporhithral (grayling region) and epipotamal (barbel region).

The shading of the floodplain by woody riparian vegetation was evaluated by a GIS analysis of orthophotos (Land NRW, 2019) which were available for the years 2008, 2011, 2014 and 2017/2018. The percentage of woody vegetation in a corridor of 30 m on each side of the streams was assessed for the lengths categories: 500 m, 2 km, 5 km, 10 km and for the whole catchment upstream of the sampling sites.

For analysis, the environmental data, that is, physico-chemical variables, substrate estimation percentages and shading percentages were standardized and z-transformed. Collinearity was explored using Variance Inflation Factor (vif function in R-package usdm). Collinear variables were subsequently removed. The remaining variables (Table S2) were then used as explanatory variables in generalized linear mixed-effects models (GLMM) applying the Imer function of the Ime4 package for R (Bates, Mächler, Bolker, & Walker, 2015). Following the cookbook of Feld, Segurado, and Gutiérrez-Cánovas (2016) the most important parameters of invertebrate changes were identified for the response variables species richness, abundance and EPT richness. The year of investigation and the streams were treated as random factors to the model to account for temporal and spatial pseudoreplication. The most parsimonious model was selected using Akaike's Information Criterion (AIC).

Non-metric multidimensional scaling (NMDS) was used to investigate community similarity patterns between the 51 samples, with Bray–Curtis similarity index applied on log(x + 1) transformed abundance data. The factor "years after restoration" was added as an overlay to the NMDS plot. The NMDS was conducted with PC-ORD version 6.22 (McCune & Mefford, 2011). Furthermore, ggplot2 package (Wickham, 2016) for R (R Core Team, 2019) was used for individual figures.



FIGURE 1 Discharge data from a gauge below the confluence of Heve and Große Schmalenau (period January 1, 2000 to July 31, 2019). HQ_1 is at 10.5 m³/s. Black arrows indicate the timing of the restoration measures. KS = Kleine Schmalenau, H = Heve, GS = Große Schmalenau

3 | RESULTS

3.1 | Site descriptors

The gauge data (Figure 1) display a typical central European discharge pattern with spring floods (February/March) and summer low flows (August/September). Mean annual discharge (MQ) of the Heve downstream of the restored section is at 1.04 m^3 /s and the 1-year high flow (HQ₁) for the last 58 years is at 10.5 m^3 /s. One extreme high flow (93.1 m³/s) was recorded in July 2007. Another high flow (20.1 m³/s) was recorded in January 2011, that is, 2 months before the second sampling and only 1 month after the first restoration measures were finalized. The next flood, which reached HQ₁, was in spring 2019.

In July and August of 2018 and of 2019, the streams experienced severe droughts and dried partly out for the first time since summer 2003.

Physico-chemical variables showed only neglectable variations between sites and years (Table 1).

Loam and clay represented a considerable percentage of the substrates in the restored watercourses, while gravel had a negative effect size (Figure S1). Macrophytes and living parts of terrestrial plants increased in percentage particularly in the second part of the 10 years study. Tree-cover decreased in the floodplains during the investigation time span due to large scale logging of the coniferous forest (Figure 2). The logging was part of a forest management plan to foster natural floodplain vegetation.

3.2 | Community descriptors

Species richness decreased strongly in the first year after restoration showing negative effect sizes in the year 2011 (Figure 3). EPT richness dropped on average by 4 taxa. In the following years, taxa numbers and EPT richness increase continuously in all three streams until 2016, suggesting recolonization of the restored sections. It took 4 years for the taxa numbers and 5 years for EPT richness to regain the values of before the restoration measures. By 2017, richness metrics decreased again. However, in the near-natural sites richness metrics followed the same trend over the time. For example, in the first year, KS-nat experienced also a loss of 10 species (5 EPT-taxa). The pattern of increase until 2016 and decrease thereafter was not as pronounced as in the restored sites. EPT richness did not regain the values of the first year of investigation.

In general, 5–10 species more inhabited the near-natural sites than the respective restored sites until 2016, by when the restored sites' species richness matched those of the near-natural sites (Figure S2).



FIGURE 2 Change of woody cover between 2008 and 2018 in the floodplains of the three streams due to extensive logging. Orthophotos by courtesy of Land NRW (2019)



FIGURE 3 Change expressed as effect size ("after" minus "before") of taxa richness, EPT richness and abundance in the three restored sites and the nearnatural sites between 2011 and 2019. Symbol/colour/linetype codes express: Triangle/blue/dashed = near-natural, circle/red/dot-dashed = restored. Wilcoxon tests showed no significant differences in richness, EPT richness or abundance in the BACI design comparing the differences of before minus after of restored sites with the before minus after of control sites [Color figure can be viewed at wileyonlinelibrary.com]

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Abundances showed similar patterns in restored and near-natural sites. They increased particularly from 2011 to 2015 and again from 2016 to 2019. The values of before the restorations were surpassed 2 years after completion, likewise in the near-natural sites.

Wilcoxon-test showed no significant differences in taxa richness, EPT richness or abundance comparing the differences of 'after' minus 'before' of restored sites with the 'after' minus 'before' of control sites.

In all three GLMM models, using taxa richness, EPT richness and abundance as response variables, the percentage of living parts of terrestrial plants and the percentage shading 500 m upstream of the sampling sites were important and often significant descriptors for the changes (Table 2). Furthermore, gravel, loam/clay and cobbles occurred in the models. AIC was low indicating a better fit in the models for taxa numbers and EPT richness (121.8 and 98.5 respectively) but high in the model for abundance (255.0).

In the first year after restoration, the community similarity to the upstream near-natural sites dropped by 31.4% in the Kleine Schmalenau and by 16.1% in the Große Schmalenau (Figure 4). In the second year after restoration, Bray-Curtis similarity directly increased

TABLE 2Best fit models forexplaining patterns in the responsevariables taxa numbers, EPT richness andabundance

| Response variable | Explanatory variables | Estimate | Std. error | t value | р |
|-------------------|-----------------------|----------|------------|---------|--------|
| Taxa numbers | Loam/clay | -3.88 | 1.07 | -3.63 | .003** |
| | Shading 500 m | -4.98 | 1.42 | -3.50 | .012* |
| | LPTP | 3.15 | 1.35 | 2.34 | .075 |
| EPT richness | Shading 500 m | -2.03 | 0.71 | -2.87 | .011* |
| | Cobbles | 2.14 | 0.79 | 2.72 | .016* |
| | LPTP | -1.09 | 0.66 | -1.64 | .140 |
| Abundance | Gravel | -184.11 | 65.89 | -2.79 | .016* |
| | LPTP | 289.46 | 118.27 | 2.46 | .028* |
| | Shading 500 m | -177.06 | 83.41 | -2.12 | .052 |

Note: The year of investigation and the sites within streams were included as random variables; significant correlations are in bold. Gravel (diameter 6–20 cm); LPTP (living parts of terrestrial plants, roots), cobbles (diameter 0.2–2 cm); shading 500 m (% shading 500 m upstream of the sampling site).

*p < .05. **p < .01.

by 26.4% and 9.7% respectively. In the following years, the similarity levelled out to on average 65%.

Over the whole 10-year period, the NMDS showed that samples of the same year of restored and respective near-natural sites cluster close to each other (Figure 5). However, samples from the first years cluster far away from samples of the later years. Additionally, when the factor "years after restoration" is overlaid on the NMDS ordination space, it aligns predominantly with axis one. This axis explains more than 47% of the variance in the long-term community composition.

The change of the invertebrate community is also observed from the longitudinal preferences of the species (Figure 6). In 2010, the mean share of epirhithral preferences (preference for small mountain brooks) was 26.2%. This decreased continuously by \sim 10% until 2019. A decrease can also be seen in the average metarhithral preferences (lower trout region). In contrast, hyporhithral and epipotamal (grayling and barbel region) preferences increased from mean values of 17.7 and 8.6%, respectively, to 21.8 and 14.1%. This change of longitudinal preferences is inherent to all sites irrespective of their restored or near-natural status.

Furthermore, epirhithral and metarhithral preferences are positively correlated to the percentage of tree cover (Table 3), while hyporhithral and epipotamal preferences are (significantly) negatively correlated to shading.

There is a phase shift of changes in longitudinal preferences following changes in shading in the 500 m segments (Figure 7). The fauna adjusts to the situation with a time lag of 1 year. Logging in the floodplain was conducted in KS-res and in H-res in winter 2010. In spring 2011, the invertebrate community shows still high preferences for epirhithral sections, while in the next 2 years the epirhithral preferences drop by more than 10%. The same trajectory is expressed in GS-res.

4 | DISCUSSION

4.1 | Restoration effects

The results reveal two different temporal patterns, a trend in the first 6 years and a trend in years 7–10. The first trend displays a set-back

of species richness, EPT richness and abundance in the first year after restoration, followed by a steady increase in the next 5 years. This trend was also found by Friberg et al. (1998) in a Danish stream, where the taxa numbers after 2 years also exceeded the initial samplings. The initial decrease can be explained by the disturbance through the heavy earthworks of the restoration measures, which nearly doubled the stream lengths in the restored sites. These restored sections were not completely recolonized 4 months after restoration, when the first sampling after restoration was conducted. However, recovery was fast and nearly completed 1 year later in the second year post-restoration. This pattern of rapid recovery was also observed by Korsu (2004). The most likely colonization pathway is downstream dispersal from the upstream near-natural sections. Many different taxa (e.g., Elmis sp., Ephemera danica, Habrophlebia sp.) established and flourished in the new habitats of the restored reaches. This is supported by Stoll, Breyer, Tonkin, Früh, and Haase (2016) who found that if local degraded stream morphology is imbedded in regional good morphology then community improvement will be most likely successful after restoration.

Overall, the system shows large changes in community composition and a high beta diversity. Interestingly, species numbers and abundances increased also in the near-natural sites, indicating that restoration was not the only factor influencing biodiversity pattern. This is supported by the results of the tests in the BACI Design. No significant differences could be found between changes in the restored sites compared to changes in the control sites. The flood in early 2011 had, together with the implementation of the restoration measures, presumably a pivotal synergistic impact on community patterns in the restored sites. Nonetheless, communities in the nearnatural sites were affected as well and lost several taxa in the first year after the flood, leading to the non-significant differences in the BACI comparison. Furthermore, the collinear results emphasize the importance of a BACI design in the investigation of restoration effects. As parallel patterns occurred of negative effect sizes in the first years and increases in the following years, the morphological instream changes in the restored sites cannot be the most important driver of community change. Notably, if only the restored sites would



FIGURE 4 Bray-Curtis similarity of the invertebrate samples of the three restored sites compared to the respective near-natural sites. Black arrows indicate the dates when the restoration measures were conducted. H-nat was not sampled in 2010

have been investigated with a before-after-comparison the results might have led to a fallacy.

Abundance patterns followed species richness patterns in the first years. Abundance increases in restored reaches were also described by Kail et al. (2015), as one of the few benthic invertebrate community patterns that changed significantly due to restoration. A potential cause for the multi-annual accrual is the flood of spring 2011, which has depleted the benthic invertebrate fauna in all sites; in subsequent years, species re-established and increased in abundance. Abundances boosting in the years after large flood events are reported several times in the literature (see Death, 2008 for a review).

Starting from 2016 species richness declined at all sites. This pattern was most probably fuelled by the summer drought of 2018, when a loss of more taxa, particularly many EPT, was observed. Beetles and dipterans were less influenced and had only minor decreases. In contrast, abundances exhibited high increases from 2016 to 2019, which was also seen by Stone and Wallace (1998) in an effective study of forest succession after logging on the invertebrate community structure. This abundance increase is particularly interesting in light of the drought of 2018. Except for some pools, the stream channels fell dry for several weeks. The majority of Central European taxa are not desiccation tolerant (Schmidt-Kloiber & Hering, 2015), thus many species obviously have not survived the drought. The recolonization was then supplemented by other taxa, particularly fostered by drifting individuals and aerial colonists like Simuliids and beetles (Brittain & Eikeland, 1988), who replaced EPT taxa. Furthermore, the logging in the floodplains reduced substantially the shading on the sampling sites, which enhanced algae growth (Noel et al., 1986). Elmidae beetles feed by grazing (Schmidt-Kloiber & Hering, 2015), thus the main food sources for the beetles flourished which may account for the increase in beetles.

Nonetheless, it can be concluded that the instream morphological restoration measures were of minor importance than the floodplain restoration measures for the benthic invertebrate community. The GLMM results highlight the importance of the tree cover for the invertebrate communities. In all three models a decrease in tree cover fostered changes in the main metrics, which were significant in taxa richness and EPT richness. Thus, the clear-cut logging was a prime driver for the variability of the invertebrate communities (Richardson & Béraud, 2014). Furthermore, percentage changes of the main habitats gravel and bank vegetation had a significant impact. The restoration measures encompassed digging new stream courses into the loam of the floodplain. Thus, in the first years loam and clay were present as substrates in the restored sites and only successively spring floods transported gravel into the sections. Bankside semiaguatic vegetation is an important biotic habitat and consecutively increased in the restored sections influencing positively taxa richness and abundance. Similar patterns of richness and abundance increases and subsequently exceeding of initial values were also experienced by Friberg et al. (1998). They assumed that river maintenance stopping was the main cause and then macrophytes increased habitat heterogeneity fostering richness and abundance. Interestingly, they found these patterns also in their control site which supports the finding of this study that floodplain management and instream biotic habitats are significant drivers of biodiversity. Additionally, Miller et al. (2010) showed that species richness responded positively to restoration in forested catchments like in this study.

4.2 | Community changes

The communities of all sites, irrespective of restored or near-natural, shifted over the 10 years sampling period. The similarity of



FIGURE 5 Joint plot of NMDS results of the invertebrate samples of the three restored sites and the respective near-natural sites and the factor "years after restoration" as overlay. The coding explains the site and the respective sampling year. Symbol/colour codes express the groups: square/blue = year before restoration and the first year after restoration and respective samples in near-natural sites; triangle/ green = second to fifth year after restoration and respective samples in near-natural sites. Samples are abbreviated according to Table 1 followed by the year in the 21st century. The sample KSres_11 was an extreme outlier and deleted from this analysis. Stress 12.4, explained variance axis 1: 47.1%, axis 2: 21.3% [Color figure can be viewed at wileyonlinelibrary.com]

communities of the same stream and year remained high, which supports the conjecture that they respond to the same external drivers, and that the communities of the paired sites (near-natural and restored) interact through upstream and downstream dispersal. Thus, time as a vector of changing catchment conditions seems to be a very important factor.

The longitudinal preferences of the invertebrate communities displayed a clear trend in the investigation period: species of upstream section decreased and species of more downstream sections increased in abundance. This pattern is consistent in restored and near-natural sites and reflects an increase in water temperature because the basis for the longitudinal preferences is water temperature preferences (Illies & Botosaneanu, 1963). This may be attributed to the loss of woody riparian cover by the logging activities in the floodplains and thus water temperatures potentially have increased due to less shading (Noel et al., 1986; Ringler & Hall, 1975). Logging activities were particularly undertaken between 2011 and 2014 and decreased the woody riparian buffer by on average 50%. Interestingly, the invertebrate communities followed the presumed increase of water temperatures with a time lag of 1 year, which is equivalent to the 1-year life cycle of most species. Thus, species preferring colder stream temperatures were replaced by species preferring warmer



FIGURE 6 Longitudinal preferences (in % of the community) of the invertebrate samples of the three restored sites and the respective nearnatural sites from 2010 to 2019. Epirhithral (preference for small mountain brooks, that is, upper trout region), metarhithral (lower trout region), hyporhithral (grayling region), epipotamal (barbel region). The black bar denotes the main logging activities in the floodplains of the streams

temperatures. This replacement is underlined by the general increase of species richness from 2011 to 2016 and the shift in community composition. A similar pattern of longitudinal preference shifts of invertebrate communities was observed by Haase et al. (2019) investigating the potential effects of global warming.

Since 2017, species richness sharply declined in the three streams which can be attributed to two other hydrologic and meteorological phenomena, a late summer flood in 2017 and a drought in summer 2018. Although the species composition seems to adapt very fast to local situations of increasing or decreasing temperatures, an unusual flood and almost completely dry river beds seem to have depleting effects. This was also shown for alpine streams and the summer drought of 2017 by Piano et al. (2019).

As part of the floodplain restoration not only logging was conducted but also reforestation. Native young alder trees have been planted and start shading the channels and provide coarse particulate organic matter for shredding invertebrates. A small increase in shading is already visible in the 2018 data for the Kleine Schmalenau. Thus, future changes in the invertebrate community are to be expected, for example, an increase of shredder to grazer percentage (Hernandez, Merritt, & Wipfli, 2005; Stone & Wallace, 1998). Furthermore, Hernandez et al. (2005) showed in Alaskan streams that alderdominated forest succession after clear-cut enhanced densities of invertebrates and led to a richer and more diverse fauna. The question remains if future shading will decrease the stream temperatures again and subsequently cold-adapted invertebrates will recolonize the sites.

5 | CONCLUSION

This 10-years consecutive data set unveils several messages.

First, a BACI design in the investigation of restoration measures is absolutely necessary. Only the comparison of changes in restored reaches with changes in control reaches unveils real responses of biotic communities to restoration efforts. Second, the more years that are investigated in restored reaches the better the knowledge of effects of external and internal factors shaping biotic communities. If only 1 or 2 years had been analysed, the importance of the high flood in spring 2011 would have been unnoticed. Thus, restoration appraisal based on one sample is not enough, because restoration effects may be masked by many other factors.

The third message is that recolonization of restored reaches can be very fast if recolonization sources are available in the close surrounding and no barriers hinder dispersal.

Fourth, local morphological restoration may affect the invertebrate community of a site but regional and landscape factors may have even higher effects. Restoration measures and their impact should always be seen in the wider context. Landcover has an overwhelming influence on invertebrate communities, as does changes in landcover. Logging of non-native trees in the floodplain as a restoration measure to reinforce native flora can have major influences on the instream fauna. **TABLE 3** Results of the correlation analysis between the percentage of shading in five different length categories and the longitudinal preferences of the invertebrate communities

| Shading length category | Epirhithral | Metarhithral | Hyporhithral | Epipotamal |
|-------------------------|-------------|-------------------|--------------|------------|
| 0.5 km | .59** | .34 ^{ns} | 58** | 58** |
| 2.0 km | .68** | .22 ^{ns} | 74** | 82** |
| 5.0 km | .67** | .15 ^{ns} | 65** | 73** |
| 10.0 km | .62** | .13 ^{ns} | 60** | 68** |
| Full catchment | .65** | .12 ^{ns} | 63** | 71** |

Note: Significant correlations are in bold. Epirhithral (preference for small mountain brooks, that is, upper trout region), metarhithral (lower trout region), hyporhithral (grayling region), epipotamal (barbel region). Abbreviation: ns, not significant.

**p < .001.



Site • GS-res + H-res + KS-res

FIGURE 7 Trajectory of the longitudinal preferences (in % of the community) of the invertebrate samples in the three restored sites in relation to the tree cover in the 500 m section of the sampling site between 2010 and 2019

Fifth, we need to think in longer time scales when evaluating restoration measures. Ten years like in this study unveiled several different patterns in the communities and several factors influencing the communities. But this will continue. Two examples, weather extremes can have severe impacts like the summer drought in 2018, and the reforestation, which presumably will alter the benthic invertebrate communities again in the coming years.

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DATA AVAILABILITY STATEMENT

The benthic invertebrate data analysed in this study are provided as supplementary material.

ORCID

Armin W. Lorenz D https://orcid.org/0000-0002-3262-6396

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