Science of the Total Environment 557–558 (2016) 722–732

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Time is no healer: increasing restoration age does not lead to improved benthic invertebrate communities in restored river reaches

Moritz Leps [a,b,*], Andrea Sundermann [a], Jonathan D. Tonkin [a,c], Armin W. Lorenz [d], Peter Haase [a,d]

[a] *Senckenberg Research Institute and Natural History Museum Frankfurt, Department of River Ecology and Conservation, Clamecy Strasse 12, 63571 Gelnhausen, Germany*
[b] *Johann Wolfgang Goethe University of Frankfurt am Main, 60629 Frankfurt am Main, Germany*
[c] *Oregon State University, Department of Integrative Biology, 3029 Cordley Hall, Corvallis, Oregon 97331, USA*
[d] *University of Duisburg-Essen, Faculty of Biology, Universitätsstrasse 5, 45141 Essen, Germany*

HIGHLIGHTS

- Restored rivers were analyzed for benthic invertebrate community change over time
- Restoration age was a poor predictor of community composition and community change
- Non-linear community shifts revealed post-restoration disturbance effects
- Catchment-scale characteristics overrode the effectiveness of river restoration
- Hydromorphological restoration alone was not sufficient to repair communities

GRAPHICAL ABSTRACT

ARTICLE INFO

Article history:
Received 26 January 2016
Received in revised form 16 March 2016
Accepted 16 March 2016
Available online xxxx

Editor: D. Barcelo

Keywords:
Macroinvertebrates
Revitalization
Species traits
Stream
Time effect

ABSTRACT

Evidence for successful restoration of riverine communities is scarce, particularly for benthic invertebrates. Among the multitude of reasons discussed so far for the lack of observed effects is too short of a time span between implementation and monitoring. Yet, studies that explicitly focus on the importance of restoration age are rare.

We present a comprehensive study based on 44 river restoration projects in Germany, focusing on standardized benthic invertebrate sampling. A broad gradient ranging from 1 to 25 years in restoration age was available. In contrast to clear improvements in habitat heterogeneity, benthic community responses to restoration were inconsistent when compared to control sections. Taxon richness increased in response to restoration, but abundance, diversity and various assessment metrics did not respond clearly. Restoration age was a poor predictor of community composition and community change, as no significant linear responses could be detected using 34 metrics. Moreover, only 5 out of 34 tested metrics showed non-linear shifts at restoration ages of 2 to 3 years. This might be interpreted as an indication of a post-restoration disturbance followed by a re-establishment of pre-restoration conditions. BIO-ENV analysis and fourth-corner modeling underlined the low importance of restoration age, but revealed high importance of catchment-scale characteristics (e.g., ecoregion, catchment size and land use) in controlling community composition and community change.

Overall, a lack of time for community development did not appear to be the ultimate reason for impaired benthic invertebrate communities. Instead, catchment-scale characteristics override the effectiveness of restoration. To

* Corresponding author at: Clamecy Strasse 12, 63571 Gelnhausen, Germany.
E-mail address: Moritz.Leps@senckenberg.de (M. Leps).

http://dx.doi.org/10.1016/j.scitotenv.2016.03.120

enhance the ecological success of future river restoration projects, we recommend improving water quality conditions and catchment-scale processes (e.g., connectivity and hydrodynamics) in addition to restoring local habitat structure.

1. Introduction

1.1. Critical issues for restoring stream integrity

River restoration is nowadays commonly applied to tackle man-made degradation of running waters that had been impaired, for example, through channelization, intensive land use and exploitation (e.g., Bernhardt et al., 2005; Nienhuis & Leuven, 2001; Woolsey et al., 2007). Owing to recent meta-analyses, however, it is common knowledge today that hydromorphological restoration alone is not sufficient to significantly improve riverine communities (Miller et al., 2010; Palmer et al., 2010; Roni et al., 2008). Many issues are discussed to be the reason for poor success of river restoration measures. Firstly, the applied restoration measures might be unable to improve the habitat quality according to the requirements of the target taxa, either generally or on the long-term (Haase et al., 2013; Palmer et al., 2010). The latter also depends on the local morphodynamics (i.e., the rate and the degree of forming and stabilizing diverse habitat features) which is in turn a function of the catchment hydrology and local flow patterns (e.g., high flow events; Januschke et al., 2014; Pasquale et al., 2011). Secondly, as most projects focus on improving in-stream structural habitat heterogeneity (Haase et al., 2013; Lave, 2009; Rosgen, 2011), the relevance of multiple stressors is often disregarded. This refers to the fact that freshwater biota in disturbed environments face numerous stressors which often act simultaneously with possible interacting effects (Leps et al., 2015; Townsend et al., 2008; Wagenhoff et al., 2011). Multiple stressors comprise intensive catchment land use, increased impervious areas, river regulation, invasive species (Allan, 2004; Sponseller et al., 2001), and climate change (Domisch et al., 2011). Coupled with these changes are, for example, increases in organic matters, nutrients, contaminants, and sediments as well as alterations to catchment hydrology, morphology and the thermal regime. Other factors are also often not considered, such as former disturbances dating back several decades (Harding et al., 1998) and short-term impacts (e.g., peak level loads of discontinuously applied agrochemicals; Larson et al., 1999) which are both difficult to discover, to monitor and to quantify. Thirdly, restoration measures are often applied at the local scale while the processes driving local disturbances, such as hydrodynamics, connectivity and the land use are operating at larger (i.e., catchment) scales and thus are unlikely to be affected by restoration (Ormerod, 2004; Robertson et al., 2014; Winking et al., 2014). In fact, river restoration may be most effective when applied in moderately degraded regions (Stoll et al., 2016). Finally, the re-establishment of target taxa might be prevented through dispersal constraints (e.g., weak dispersal abilities of the taxa) and landscape constraints including a high degree of ecosystem fragmentation and lacking connectivity to neighboring source populations (Kappes & Haase, 2012; Sundermann et al., 2011; Tonkin et al., 2014). Moreover, rarity of the target taxa (Biggs et al., 1998, Langford et al., 2009), and the occupation of ecological niches with tolerant pre-restoration communities (i.e., competition filter; Ormerod, 2004; Spänhoff & Arle, 2007) will probably limit the success of river restoration.

1.2. Restoration age, an understudied factor

The time since restoration (i.e., restoration age) has often been discussed but rarely studied as a possible reason for the lack of improved benthic communities. This is surprising, since the understanding of ecological succession in running waters teaches us, that the development of habitat features, local flow patterns and hydraulics, in-stream and riparian vegetation, as well as the recolonization of habitats will require time after any disturbance (refer to Ward et al., 2002). This applies also to the restoration of rivers, which induce ecosystems to leave their actual states and to enter processes of dynamic succession, which involve coupled changes in abiotic environmental factors and inhabiting communities (Dufour & Piégay, 2009). It is still unknown which periods of time are required for this succession process before attaining a new equilibrium-like status which is ideally more natural compared to pre-restoration conditions (Januschke et al., 2014). Yet, complex and unpredictable recovery dynamics may lead to endpoints dissimilar to the pre-degradation state of the community condition, causing the conventional idea of restoration success to fail (Dufour & Piégay, 2009; Lake et al., 2007; Sarr, 2002). Moreover, considerable time lags between completion of the restoration measures and ecological recovery (i.e., hysteresis effects) may result in monitoring programs missing these changes due to the lack of time for the restored sites to mature (Januschke et al., 2014; Jones & Schmitz, 2009; Winking et al., 2014). This may apply especially whenever positive effects of the restoration measures have to be passed through complex food webs or processes acting at large spatio-temporal scales (Ormerod, 2004). Therefore, the restoration age is a crucial factor to consider when monitoring the results of restoration on riverine communities (Bash & Ryan, 2002).

1.3. Research objectives

Here, we present a comprehensive study on 44 hydromorphological river restoration projects in Germany using a rigorous study design, highly standardized sampling methods and covering a broad gradient of restoration ages (1–25 years). This design allows for the first time to follow post-restoration community changes along a temporal gradient. The following objectives were addressed: (1) assess general community responses to restoration using a space-for-time substitution approach, (2) identify linear and non-linear time patterns of community recovery and equilibration, and (3), since influential factors on community change are well known to be manifold, investigate the importance of the restoration age in interaction with confounding environmental factors and species traits.

We tested the following hypotheses: (i) after the initial recovery time from the disturbance caused by the restoration measures, community responses will increase with time since restoration to a certain point. However, (ii) community responses over time will be generally weak as they are overridden by confounding factors such as catchment-scale characteristics (e.g., land use) and species traits.

2. Methods

2.1. Investigated sites

Our survey included 44 hydromorphological river restoration projects located in Germany (Fig. 1). The dataset covered 31 river restoration projects in hilly-mountainous region (mean elevations of 197 $\pm$ 85.6 (SD) m asl and catchment sizes of 153 $\pm$ 506 km^2), and 13 located in lowlands (68.8 $\pm$ 41.5 m asl; 621 $\pm$ 891 km^2). The river restoration projects had been selected for having undergone comprehensive hydromorphological restoration measures that are common techniques in central European restoration practices and for being well documented with respect to aspects including year of restoration, type of measures undertaken, location and length of restored reach. With this, the selected projects were representative for a large number of

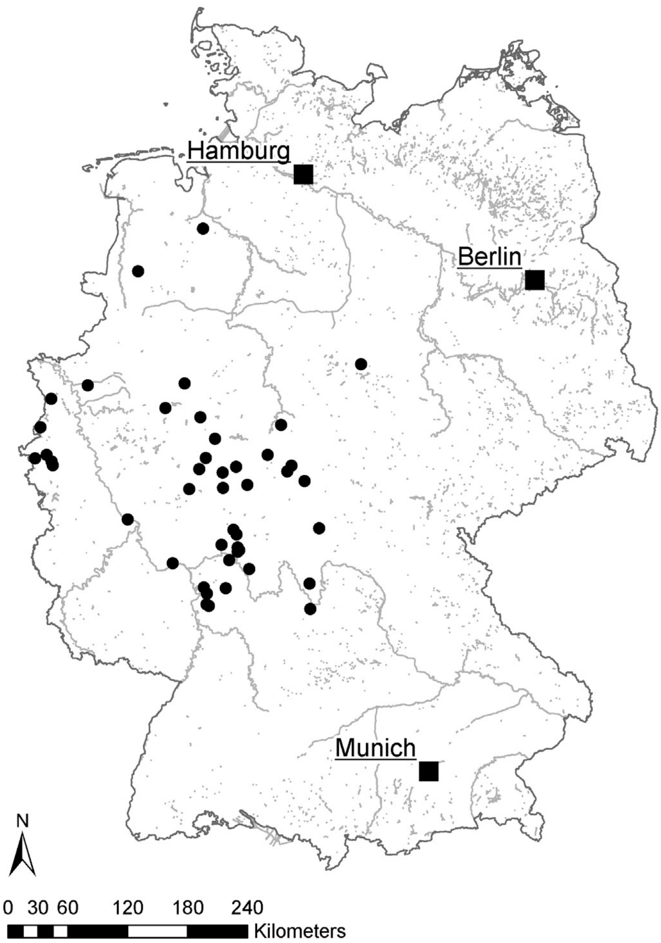


Fig. 1. Location of the restoration project sites in Germany.

hydromorphological restoration projects conducted all over central Europe in the past 25 years. To avoid any replication, multiple river restoration projects of the same river were only included in the case of a change in stream type between sites.

The restoration measures conducted at the sites were diverse, including at least 1 and up to 8 of the measures given in Table 1 (see also Appendix A for project-specific information). The restoration age (time period between completion and sampling) ranged from 1 to 25 years with a mean restoration age of 7.9 ± 5 years.

Table 1
Restoration measures, central goals and other characteristics and of the investigated restoration projects.

Restoration measures	
Stream bed	Installation of flow deflectors (addition of large wood, logs and boulders)
	Habitat enhancement (dead wood addition)
	Uplifting of incised stream beds
Stream banks	Removal of bank fixations
	Reconnection of back waters
	Construction of new water courses and secondary channels
Floodplains	Extensification of floodplain land use
Other characteristics	
Central project goals (as reported by water managers)	Increased physical habitat heterogeneity
	Prevention of floods
	Improved longitudinal connectivity
Mean length of restored reaches	1 ± 0.8 km (maximum: 3.3 km)
Years of completion	1988–2012

2.2. Space-for-time substitution

Due to the lack of pre-restoration data, a space-for-time substitution approach was conducted. Within the restored reaches, a 100-m-long section was selected for investigation (restored section). Additionally, for each of the restoration projects, a second 100-m-long non-restored section was chosen in the same river (i.e., control section) which was usually located upstream and with a mean flow distance of 1.6 ± 1.9 km to the restored section. The control sections were carefully selected to be representative for the pre-restoration status of the restored sections in terms of stream type, stream order, water quality and local land use patterns (no confluences of tributaries, point source discharges, lakes, fish ponds or impoundment basins were between the two sections). Each restoration project (both sections) was sampled once at a specific time since restoration. Detailed information on the sampling procedure is given below.

2.3. Benthic invertebrates

Both restored and control sections were sampled once for benthic invertebrates according to the standardized protocol for collecting samples in river monitoring programs to assess the ecological status of rivers in Germany (Haase et al., 2004). Samples were collected from March to July in period 2006–2014. A multi-habitat sampling approach was taken, where all of the microhabitats in the 100-m-long section were recorded in 5% coverage intervals and each 'sampling unit' (25 × 25 cm) was sampled using a handnet (opening: 25 × 25 cm; mesh size: 0.5 mm). We applied the kick sampling method according to Barbour et al. (1999). A complete sample comprised 20 sampling units that were pooled for further analysis (total sampling area of 1.25 m^2). The organisms were sorted in the laboratory and identified to a taxonomic level defined by the 'Operational Taxalist for Running Waters in Germany' (Haase et al., 2006).

Abundances (number of individuals per m^2) and 33 additional metrics were calculated for each sample (Table 2, Hering et al., 2004a). All metrics were calculated with the software ASTERICS, Version 4.04 (http://www.fliessgewaesserbewertung.de/download/berechnung).

2.4. Hydromorphology

For a subset of 36 restoration projects, hydromorphological data was recorded on 10 transects at intervals of 10 m within the 100-m-long stream sections (both restored and control sections). Aquatic microhabitat characteristics including substrate type (Hering et al., 2003), depth and current velocity (coded in 6 discrete velocity classes) were recorded at 5 or 10 intervals along each of the 10 transects, depending on river width. Moreover, mesohabitat characteristics of the rivers and their floodplains were recorded on each transect (Jähnig et al., 2008), including bankfull height and width, channel width and number and type of channel features (e.g., multiple channels, gravel bars, islands, dead wood, trunks). From these characteristics, 8 aggregated metrics were derived (Table 2). The variables incision and steepness were available only for 25 and 24 restoration projects, respectively.

2.5. Land use

Catchment areas of the sites were delineated (ArcGIS 10.3 for Desktop, 1999–2014 Esri Inc.) from a digital elevation model (grid size 25 m) while Corine Land Cover (CLC) classes (CLC2006, German Environmental Agency, DLR-DFD 2009; Keil et al., 2010) were used to derive upstream catchment land use. The CLC classes were grouped into the following categories: (1) artificial surfaces (CLC class 1), (2) arable land and permanent crops (CLC classes 2.1 and 2.2) and (3) pastures and heterogeneous agricultural areas (CLC classes 2.3 and 2.4). The remaining cover is comprised of forest and other natural land cover (CLC classes 3–5). For use in the calculations, land cover was quantified

Table 2
Benthic invertebrate community metrics and hydromorphological metrics used in the present study.

Metrics	Metric class[a]	Metric description
Benthic invertebrate community metrics		
Abundance	C/A	Individuals per m^2
%Ephemeroptera	C/A	Ephemeropterans, % of abundance
%EPT	C/A	EPT-taxa, % of abundance
%Plecoptera	C/A	Plecopterans, % of abundance
%Trichoptera	C/A	Trichopterans, % of abundance
%Epirhithral	F	% of epirhithral-taxa
%Hyporhithral	F	% of hyporhithral-taxa
%Metapotamal	F	% of metapotamal-taxa
%Cobble	F	% of cobble[b] dwelling taxa
%Gravel	F	% of gravel[b] dwelling taxa
%ActFilFeed	F	% of active filter feeders
%GathCol	F	% of gatherers and collectors
%GrazScrap	F	% of grazers and scrapers
%PasFilFeed	F	% of passive filter feeders
%Predators	F	% of predators
%Shredders	F	% of shredders
%Xylophagous	F	% of xylophagous taxa
Rheoindex	F	Dominance of rheophilic taxa[c]
Num. Taxa	R/D	Number of taxa
Num. Genera	R/D	Number of genera
Num. Families	R/D	Number of families
Num. EPT	R/D	Number of EPT-taxa
Num. EPTCBO	R/D	Number of EPTCBO-taxa
Simpson Div.	R/D	Simpson diversity index[d]
Shannon Div.	R/D	Shannon-Wiener diversity index[e]
Evenness	R/D	Evenness of Shannon-Wiener-diversity[f]
BMWP	S/T	Biol. Monitoring Working Party[g] score (sum of family-level tolerance scores against organic pollution)
ASPT	S/T	Average Score per Taxon[g] (BMWP divided by number of scoring families)
Faunaindex (FI)	S/T	Dominance of stream-type specific indicator taxa[h] (indicates hydromorphological degradation)
FI class 1 taxa	S/T	Number of strong indicator taxa used for Faunaindex[h]
FI class 2 taxa	S/T	Number of very strong indicator taxa used for Faunaindex[h]
GSI	S/T	German Saprobic Index[i] (indicates organic pollution)
MMI	S/T	Multi metric index[j] (German national metric; indicates general degradation)
EQC	–	Ecological Quality Class[j] (One of five ecol. Status classes according to EU-WFD[k,l], derived from MMI)
Hydromorphological metrics		
Incision	–	Bankfull height divided by bankfull width
Steepness	–	Steepness of banks (bankfull height divided by bank width)
CV_bank	–	Coefficient of variation (CV) of bankfull width
CV_channel	–	CV of channel width
N_features	–	Number of channel features
D_features	–	Shannon-Wiener diversity index[d] of channel feature composition
CV_velocity	–	CV of current velocity
CV_depth	–	CV of river depth
N_substrate	–	Number of substrate types
D_substrate	–	Shannon-Wiener diversity index[d] of substrate composition

[a] C/A: composition/abundance; F: functional; R/D: richness/diversity; S/T: sensitivity/tolerance.
[b] Gravel: grain size 0.2–2 cm; Cobbles: grain size >2 cm.
[c] Banning (1998).
[d] Shannon (1948).
[e] Simpson (1949).
[f] Pielou (1966).
[g] Armitage et al., (1983).
[h] Lorenz et al. (2004).
[i] Friedrich & Herbst (2004) and Rolauffs et al. (2004).
[j] Böhmer et al. (2004).
[k] EU Commission, 2000.
[l] Hering et al., 2004b.

as proportional coverage (percentages) of the non-natural land use classes based on the catchment area. From these data, a Land Use Index (LUI) was derived according to the following equation (Böhmer et al., 2004): LUI = pastoral cover [%] + 2 arable cover [%] + 4 artificial cover [%].

2.6. Calculations

For our analyses we used a broad variety of statistical methods and approaches. Only a very brief description is provided in the following section, with a full description provided in the supplementary material (Appendix B).

Initially, we checked whether the hydromorphological conditions of the sites were directly affected by the restoration efforts by comparing hydromorphological metrics of the restored and control sections (paired Wilcoxon tests; Wilcoxon, 1945). Community responses to restoration (research objective 1) were analyzed using PERMANOVA analysis to test for differences in the community composition of restored and control sections (Anderson, 2001; Oksanen et al., 2015).

The exclusive effect of increasing restoration age on the community structure and the community metrics (research objective 2) was tested using three approaches. Firstly, the Bray-Curtis distances of paired control and restored sections and the community metrics' differences (restored minus control) were analyzed for linear trends with increasing restoration age using simple linear regression analysis. Secondly, these data were analyzed for non-linear change points in terms of significant shifts in the mean at specific restoration ages. Thirdly, to support evidence on the change points identified by the former approach, the data was additionally analyzed using recursive partitioning (R package rpart; Therneau & Atkinson 1997; Therneau et al., 2015).

The combined role of restoration age and environmental variables in explaining changes in the community composition (research objective 3) was assessed using BIO-ENV analyses and Mantel tests (R package vegan; Clarke & Ainsworth, 1993; Legendre & Legendre, 1998; Oksanen et al., 2015). In these analyses we used two approaches based on two different data matrices (A: all projects and 5–6 variables; B: a subset of projects and 5–6 variables plus hydromorphological metrics). Three models were built for each approach, using square-root transformed abundance data (1) of the restored sections only, (2) of both the restored and control sections, and (3), using changes in taxon presence when comparing control and restored sections. Finally, we assessed how taxon-specific variability of responses on increasing restoration ages depended on species' traits (body size, dispersal ability, life cycle duration, feeding habit and substratum preference). This was done using the mvabund package for R (model-based analysis of multivariate abundance data; Wang et al., 2012; Wang et al., 2015), which builds on generalized linear models (GLM) and provides a framework to approach the 'fourth-corner problem' by fitting models for species abundance as a function of environmental variables, species traits and environmental-trait interactions (Brown et al., 2014). The environmental-trait interaction model was fit using the LASSO penalty (Tibshirani, 2011).

All statistical analyses were performed in R version 3.1.2 (R Core Team, 2014).

3. Results

The comparison of the hydromorphological metrics between the control and restored sections revealed significant differences for all metrics (Table 3). The large majority of the restored sections were less incised, had lower gradient banks and the micro- and mesohabitat characteristics were more diverse.

Table 3
Comparison of the hydromorphological metrics between control and restored sections. The number of restoration projects available for comparison are given (N) as well as the mean values of the control and restored sections, the mean difference (restored minus control), significance (paired Wilcoxon test) and the numbers of projects with negative (N −), neutral (N 0) and positive (N +) differences in the metrics. Asterisks indicate significant results $^{***}P \leq 0.001$, $^{**}P \leq 0.01$, $^{*}P \leq 0.05$. For description of the metrics, see Table 2. CV: coefficient of variation, D: Shannon-Wiener diversity, N: number.

Hydromorphological metric	N	Control	Restored	Difference	*P*-value	N −	N 0	N +
Incision	25	0.09	0.03	−0.07	<0.001***	25		
Steepness of banks	24	0.46	0.18	−0.28	<0.001***	22		2
CV_bank	36	0.11	0.24	0.13	<0.001***	5		31
CV_channel	36	0.10	0.21	0.11	<0.001***	5		31
N_features	36	2.42	5.64	3.22	<0.001***	3	2	31
D_features	36	0.67	1.38	0.71	<0.001***	3	1	32
CV_velocity	36	0.32	0.43	0.11	0.002**	11	1	24
CV_depth	36	0.42	0.49	0.06	0.007**	10		26
N_substrate	36	5.42	6.69	1.28	0.004**	9	3	24
D_substrate	36	1.05	1.26	0.20	0.003**	13		23

3.1. Community responses to restoration

Across projects, the overall community change varied from 0.269 to 0.703 with an average of 0.43 ± 0.11 (Bray Curtis distance). Nevertheless, the community composition did not differ significantly between restored and control sections (PERMANOVA, df = 1, 86; F = 0.413; $R^2 = 0.005$; $P = 0.999$).

The comparison of 34 community metrics revealed significant positive differences for five richness metrics (number of taxa, genera, families, EPT- and EPTCBO-taxa) and the two sensitivity/tolerance indices BMWP and ASPT (Table 4). The taxon richness increased significantly from 34 to 38.1 taxa with the EPT- and EPTCBO-taxa being mainly responsible for these gains, while showing strong turnover. For all other metrics, differences were highly variable and outweighed between sites with positive and negative changes (e.g., GSI), or neutral with the majority of restored sections showing no change at all (e.g., EQC).

Table 4
Comparison of the community metrics between control and restored sections. The mean values of the control and restored sections are given as well as the mean difference (restored minus control), significance (paired Wilcoxon test) and the numbers of projects with negative (N −), neutral (N 0) and positive (N +) differences of the metrics. All 44 restoration projects were included in this comparison. Asterisks indicate significant results $^{***}P \leq 0.001$, $^{**}P \leq 0.01$, $^{*}P \leq 0.05$.

Metric	Control	Restored	Difference	*P*-value	N −	N 0	N +
Abundance	1350	1769	419	0.283	21		23
%EPT	24.0	21.9	−2.12	0.768	19		25
%Ephemeroptera	13.5	11.8	−1.75	0.428	24		20
%Plecoptera	2.90	2.56	−0.33	0.438	13	21	10
%Trichoptera	7.61	7.57	−0.04	0.949	22		22
%Epirhithral	7.14	6.76	−0.38	0.158	27		17
%Hyporhithral	12.6	12.5	−0.06	0.322	24		20
%Metapotamal	5.19	4.82	−0.36	0.294	25		19
%Gravel	6.87	7.23	0.36	0.849	21		23
%Cobble	18.1	18.4	0.38	0.903	22		22
%ActFilFeed	5.50	5.22	−0.28	0.682	20		24
%GathCol	32.2	32.9	0.62	0.435	20		24
%GrazScrap	16.7	15.2	−1.50	0.673	22		22
%PasFilFeed	4.05	6.70	2.65	0.092	20		24
%Predators	9.51	9.39	−0.12	0.949	20		24
%Shredders	19.6	17.3	−2.31	0.123	25		19
%Xylophagous	0.13	0.10	−0.03	0.383	15	20	9
Rheoindex	0.59	0.61	0.02	0.352	20	1	23
Num. Taxa	34.0	38.1	4.14	0.0011**	10		34
Num. Genera	28.3	30.4	2.14	0.026*	14	3	27
Num. Families	21.4	23.1	1.70	0.009**	10	3	31
Num. EPT	12.8	14.6	1.89	<0.001***	7	7	30
Num. EPTCBO	17.3	20.4	3.09	<0.001***	11	3	30
Simpson Div.	0.80	0.80	0	0.243	19		25
Shannon Div.	2.28	2.34	0.06	0.203	19		25
Evenness	0.65	0.65	0	0.683	21		23
ASPT	5.57	5.71	0.15	0.048*	18		26
BMWP	105	117	11.5	0.0013**	13		31
FI	0.46	0.44	−0.02	0.440	22	4	18
FI class 1 taxa	4.86	5.45	0.59	0.309	17	8	19
FI class 2 taxa	2.64	2.82	0.18	0.497	14	10	20
GSI	1.95	1.95	0	0.959	21	3	20
MMI	0.43	0.43	−0.01	0.717	20	5	19
EQC	3.34	3.34	0	1	8	28	8

3.2. Linear and non-linear time patterns of community recovery

Bray-Curtis distance was positively but non-significantly related to restoration age. Similarly, no significant linear relationships were found between the restoration age and the community metrics' differences (restored minus control, Fig. 2).

Only 5 out of the 34 community metrics revealed significant non-linear shifts in the mean difference (restored minus control) at restoration ages of 2 to 3 years, while no shift could be observed in the Bray-Curtis distance (Fig. 3). The recursive partitioning analysis identified non-linear age splits for 9 of the community metrics (vertical lines in Fig. 3). For 4 of these metrics, the shift was congruent with the ones identified using the first approach.

In the case of %Epirhithral, %Ephemeroptera and %EPT, negative mean values were found for restoration ages lower than the identified age split, with a significant shift to approximately zero for higher restoration ages. In contrast, %Shredders and the Faunaindex showed positive mean values below the age split and negative above. In spite of high response variability, the effect sizes (Cohen's D) of significant age splits were large (>0.8; cf. Cohen, 1988) and ranged from 0.83 to 1.25.

3.3. The importance of environmental factors and species traits

The BIO-ENV analyses revealed maximum rank correlations between the community dissimilarity matrix and the best subset of the benthic invertebrate community and hydromorphological metrics (explanatory variables, Table 2) ranging from 0.14 to 0.34 while approach B performed best (Table 5). The restoration age, only relevant for models A1, B1, A3 and B3, was selected only in B1, but with low explanatory value and no significance assigned to by the Mantel test. The variable 'restored' (yes or no; relevant to models A2 and B2) did not contribute to the best subsets of explanatory variables. Distances of the LUI revealed high importance in explaining community dissimilarities, just as some hydromorphological variables (e.g., CV_velocity).

Selected species traits were available for 319 out of 380 taxa (body size, dispersal ability, life cycle duration, feeding habit and substratum preference). Ninety-seven out of these 319 taxa occurred at least at 10% of the investigated sites and thus were available for the multivariate and fourth-corner modeling. A multivariate GLM based on the variables age, ecoregion, catchment size, MMI_control, LUI and interactions of the last four variables with age, explained 12.6% of variance (McFadden's likelihood-ratio index; McFadden, 1974). Resampling-based ANOVA supported the significance ($P = 0.001$) of this model compared to the intercept-only model, but only two variables contributed significantly

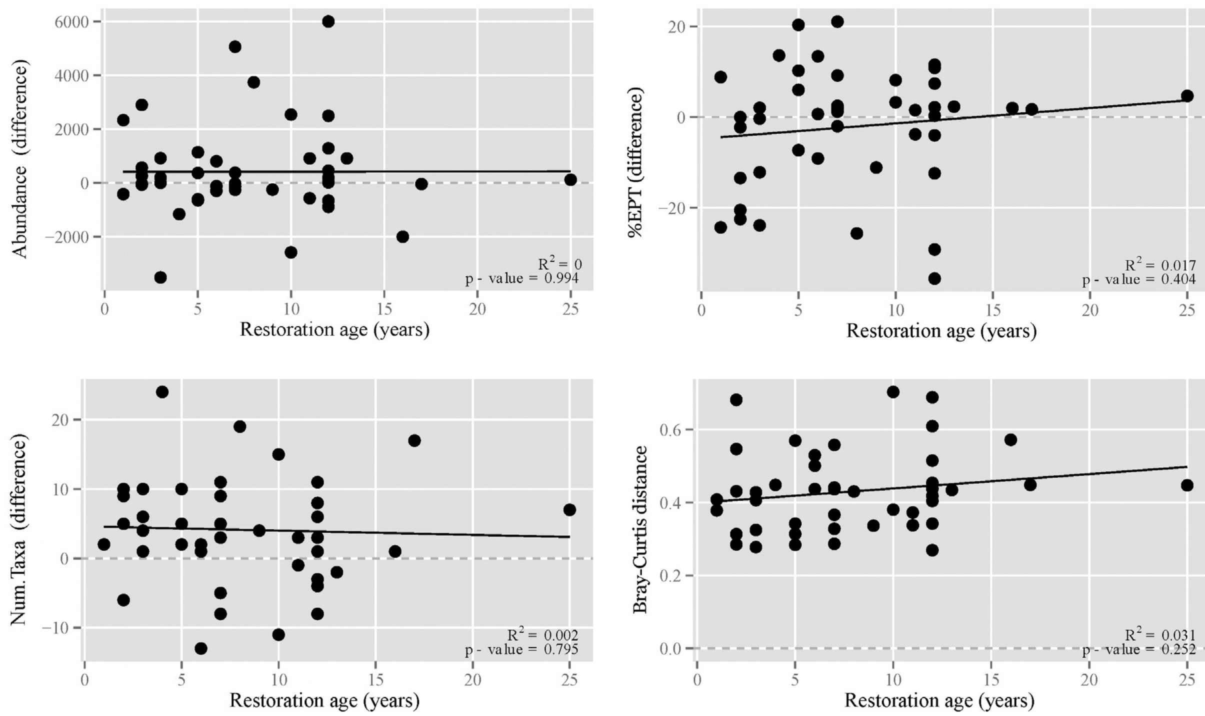


Fig. 2. Simple linear least squares regression analysis of the differences (restored minus control) in taxon abundance, %EPT, Num. Taxa and the Bray-Curtis distance (only four plots are shown as examples). *R*-squared and *P*-values are given.

to the explanation of the variance (ecoregion, $P = 0.031$; catchment size, $P = 0.011$). The remaining variables and the AGE-interaction terms were non-significant ($P > 0.05$). The fourth-corner model revealed significance for the species traits in explaining the variation in environmental responses across species ($P = 0.001$). Several of the interaction coefficients were set to zero during model shrinking via the LASSO penalty (Table 6). The highest impact was found for trait interactions with the MMI_control variable. The dispersal metric and the substratum preference metric 'macrophytes' achieved the highest average interaction coefficients across the tested variables. Refer to the Supporting Information for multivariate model coefficients (Appendix C).

4. Discussion

Based on a comprehensive data set and a rigorous study design we showed that the restoration measures could well improve the hydromorphological conditions. In particular, there was evidence for improved habitat diversity and lateral connectivity (i.e., rivers were less incised). These results are in line with previous studies like Haase et al. (2013), who found significantly recovered hydromorphological parameters in restored sites that were generally matching the degree of improvements that can be expected for restored rivers (Kamp et al., 2007) although not complying with reference conditions. Januschke et al. (2014) equally reported improved diversity of channel features, but microhabitat characteristics were less affected by restoration. Therefore, it is still unclear whether the detected improvements are qualitatively and quantitatively sufficient to enhance community integrity and diversity.

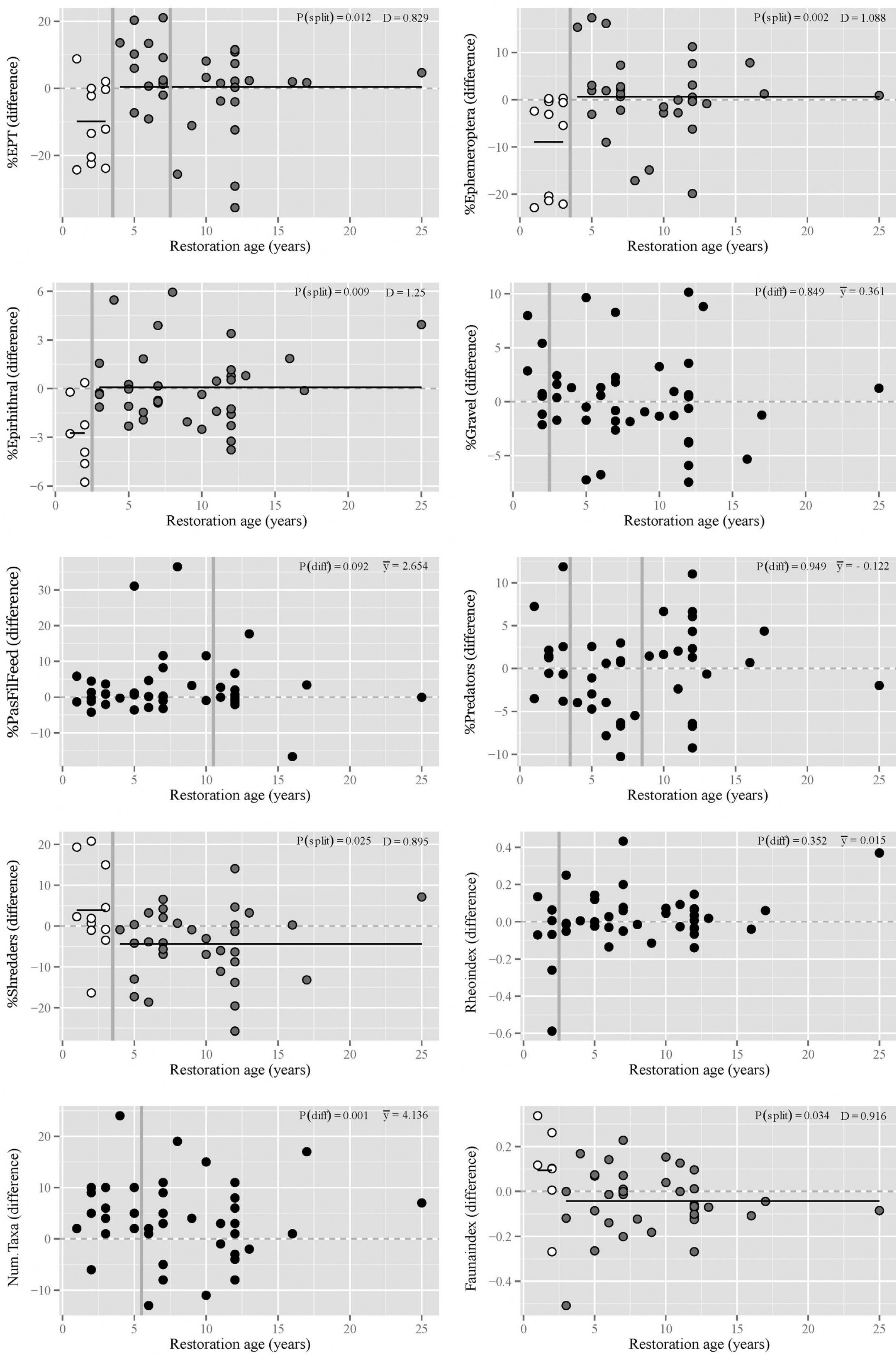
4.1. Community responses to restoration

Benthic invertebrate community responses to restoration were highly variable. In spite of a considerable species turnover and increased taxon richness, neither diversity measures nor taxon abundance responded significantly. While increased taxon richness has been supposed to enhance resilience and ecosystem functionality, higher trophic levels and neighboring ecosystems might not benefit unless the density increases, favoring enhanced transfer of biomass and energy (Baxter et al., 2005; Miller et al., 2010). The metrics of the German assessment system (comprised of the Rheoindex, GSI, Faunaindex and MMI) also remained generally unaffected. Our results are consistent with those of other studies that found a high variability in the response of benthic invertebrates to hydromorphological restoration, but no directed changes, let alone improvements in the assessment results in spite of clearly enhanced hydromorphological quality (Bernhardt & Palmer, 2011; Haase et al., 2013; Palmer et al., 2010).

4.2. Linear and non-linear time patterns of community recovery

In spite of a broad gradient in restoration age, this factor did not show any significant linear effects neither on the overall community shift nor on changes in the community metrics' differences. Moreover, non-linear effects (i.e., significant age splits) were equally absent for the vast majority of metrics. These results are in line with studies that have demonstrated missing improvement and ongoing species turnover in riverine communities even after several years post restoration (Fuchs & Statzner, 1990; Januschke et al., 2014; Nilsson et al., 2015) and others that found the community changes to be independent on the restoration age (Doll et al., 2015; Miller et al., 2010). Similarly, a recent meta-analysis of restored wetlands worldwide found the restoration age was not an important predictor of biodiversity and ecosystem services provided by restored sites (Meli et al., 2014).

As implied by our first hypothesis, however, we found evidence for both community disturbance and recovery following the restoration event. One the one hand, the dominance of Ephemeroptera, EPT- and Epirhithral-taxa decreased towards conditions dissimilar from the control section during the first 2 to 3 years after completion. This likely reflects the disturbance effect that construction works of river restoration projects can have, favoring traits typical for disturbed environments (Louhi et al., 2011; Spänhoff & Arle, 2007; Tullos et al., 2009). Such restoration approaches typically include major earthworks altering local conditions detrimentally in the short term. This includes changes in flow patterns, morphodynamics, the loss of shading and


%EPT (difference)
P(split) = 0.012 D = 0.829
Restoration age (years)
%Ephemeroptera (difference)
P(split) = 0.002 D = 1.088
Restoration age (years)
%Epirhithral (difference)
P(split) = 0.009 D = 1.25
Restoration age (years)
%Gravel (difference)
P(diff) = 0.849 ȳ = 0.361
Restoration age (years)
%PasFilFeed (difference)
P(diff) = 0.092 ȳ = 2.654
Restoration age (years)
%Predators (difference)
P(diff) = 0.949 ȳ = - 0.122
Restoration age (years)
%Shredders (difference)
P(split) = 0.025 D = 0.895
Restoration age (years)
Rheoindex (difference)
P(diff) = 0.352 ȳ = 0.015
Restoration age (years)
Num. Taxa (difference)
P(diff) = 0.001 ȳ = 4.136
Restoration age (years)
Faunaindex (difference)
P(split) = 0.034 D = 0.916
Restoration age (years)

often the transition from heterotrophy towards autotrophy (McMillan et al., 2014; Sweeney et al., 2004; Tullos et al., 2009).

On the other hand, the dominance of Ephemeroptera, EPT- and Epirhithral-taxa re-approached to approximately control conditions after 2 to 3 years. Thus, a quick and migration-driven reestablishment of pre-restoration community structure with taxa originating from nearest surroundings (i.e., degraded sections) might have occurred, as it was expected by Lorenz et al. (2009) in the absence of more natural species pools. Likewise, a study of Laasonen et al. (1998) found stagnating trends in benthic abundance within restored reaches following an initial, rapid phase of recolonization, which was probably originating from refuges within the restored reach and the immediate surroundings (Spänhoff & Arle, 2007). Generally, there is empirical evidence that recolonization can occur quickly (cf. Gore & Milner, 1990; Gustafsson et al., 2013; Winking et al., 2014) with migration occurring mainly within the first few kilometers of flow distance (Sundermann et al., 2011; Tonkin et al., 2014). This supports our assumption that colonizers mainly stem from the degraded sections.

Recovery from bed disturbance in streams has been shown to be dependent on productivity, or the recovery of the autotrophic food supply (Death and Zimmermann 2005; Tonkin and Death 2012). We did not measure periphytic algal biomass here, but that potentially represents an important factor governing the response times to these restorative procedures opening the river up to autotrophy. The riparian vegetation, however, cannot be expected to evolve considerably over 2 to 3 years (Pasquale et al., 2011) and thus to trigger the observed community shifts. For instance, Howard-Williams & Pickmere (1994) and Davies-Colley et al. (2009) showed that maturation of woody riparian vegetation after restoration, the reestablishment of canopy cover and shading, and the provision of dead wood and leaf litter requires much longer periods of time (i.e., decades). Accordingly, the observed shifts in dominance of the shredders can be hardly explained with changes of instream and riparian vegetation. While the loss of shading and increased macrophytes might have favored those taxa, their decrease after 3 years is more likely to be driven by relative gains of EPT-taxa than by maturation of the vegetation.

Our findings can be related with recent research (Li et al., 2015), where the dispersal capacity of restored river reaches (i.e., the abundance-weighted sum of the taxa's dispersal abilities) was shown to decrease during 1 to 10 years after restoration with the strongest rate in the first 3 to 4 years. Li et al. (2015) concluded that strong dispersers, already present immediately after restoration, were subsequently joined by colonizing weak dispersers, which reduced the overall dispersal capacity of the communities.

4.3. The importance of environmental factors and species traits

While BIO-ENV analysis also indicated a weak influence of restoration age on both community composition at the restored sections and on community shifts from control to restored sections, some hydromorphology metrics were strongly linked to community composition. Given only a few biological metrics indicated improved benthic communities following restoration, improved micro- and mesohabitat characteristics remain insufficient to increase community integrity. Instead of inducing directed changes in the community composition towards improved community metrics, the investigated hydromorphology metrics appeared to induce complex and multidirectional effects on the community composition. However, we point out that the results of future research might become clearer when including further hydromorphology and hydrology metrics, such as the frequency and intensity of high flow events.

Table 5
Results of the BIO-ENV analysis and Mantel tests. Refer to Table 2, Appendices B, C and section 1.6 (Calculations) for explanation of the variables and models. The results are displayed in a cumulative way, i.e., with variables of the best subset added subsequently with increasing cumulative rank correlation (ρ cum.) to the community dissimilarity matrix from top to bottom. Asterisks indicate significant models $^{***}P \le 0.001$, $^{**}P \le 0.01$, $^{*}P \le 0.05$. CV: coefficient of variation, D: Shannon-Wiener diversity, N: number.

Approach A $n = 44$	BIO-ENV analysis		Mantel test
	Model	ρ cum	*P*-value
A1 restored sections	Catchment size	0.097	0.109
	+ MMI_control	0.148	0.022*
	+ LUI	0.220	0.002**
A2 all sections	Catchment size	0.112	0.025*
	+ LUI	0.199	0.001***
A3 change in presence/absence	Catchment size	0.252	0.018*
Approach B $n = 36$			
B1 restored sections	Age	0.047	0.225
	+ Catchment size	0.083	0.165
	+ MMI_control	0.156	0.021*
	+ CV_velocity	0.202	0.008**
	+ LUI	0.275	0.001***
	+ D_features	0.340	0.001***
B2 all sections	CV_velocity	0.080	0.049*
	+ Catchment size	0.114	0.039*
	+ Ecoregion	0.166	0.002**
	+ LUI	0.206	0.001***
B3 change in presence/absence	LUI	0.092	0.161
	+ D_features	0.175	0.026*
	+ CV_velocity	0.239	0.003**
	+ Catchment size	0.301	0.001***

In support of our second hypothesis, restoration effects tended to be overridden by, for instance, the influence of intensive land use, which was characteristic for many catchments investigated in the present study (arable land use: up to 96.9%, on average 27.8 ± 22.9%; artificial land use: up to 45.3%, on average 9 ± 8.1%). These results are in line with recent studies suggesting the local hydromorphology is a weak driver of community condition in a multiple stressor environment (e.g., Miller et al., 2010; Sundermann et al., 2013). In our study, both mitigating effects of improved local hydromorphology and revegetated riparian buffer strips were clearly shown to be overwhelmed by the influence of catchment-wide land use (see also Leps et al., 2015). Therefore, prior or at least in parallel to restoring local habitat conditions, it is essential to improve the water quality (e.g., nutrient loads and toxicants) and to mitigate overriding watershed-scale processes (Roni et al., 2008). Nevertheless, Stoll et al. (2016) indicate that the best place to focus restoration efforts to exert the strongest biotic response may be in regions with intermediate levels of impairment. Moreover, we found that the community composition and its shift in response to restoration was clearly dependent on the given stream type (i.e., ecoregion and catchment size), which highlights the amount of between-project variability inherent to the investigated study sites. This gives support to the advice of Dufour & Piégay (2009) and Leps

Fig. 3. Identified non-linear shifts in the metrics' differences (restored minus control) against the restoration age. Only 10 out of 34 tested community metrics are shown, where a significant ($P \le 0.05$) difference between the group means (black horizontal lines) were found and/or where the data could be partitioned into two or more groups via the recursive partitioning approach (grey vertical lines). In cases of significant shifts in the mean, data points with restoration ages lower than the identified age split are shown with open circles and older ones have filled circles. *P*(split): *P*-value of the Mann-Whitney *U* test for differences in group means; D: Cohen's D; P(diff): *P*-value of the paired Wilcoxon-test for the metrics' differences being unequal to zero (see Table 4); $\bar{y}$ overall mean value.

Table 6
Coefficients of the environmental vs. species trait interactions in the fourth-corner modeling. Each value indicates the amount by which a change of 1 SD in the trait variable changes the coefficient of the given environmental variable. Interaction terms that were set to zero (LASSO) are printed in grey. The remaining ones are highlighted in different shades of grey ranging from light to dark grey with increasing absolute values. In case of the ecoregion, coefficients of the factor level 'lowland' are shown.

Species trait group	Species trait	Age	Ecoregion	LUI	Catch. size	MMI control
Body size	Max. potential size	0.016	0	0.083	0	-0.153
Dispersal ability	Dispersal metric	0	-0.071	0	0.113	0.287
Life cycle duration	< 1y	0	-0.045	0	0	0.032
Life cycle duration	> 1y	-5E-04	0	0	0.018	-0.008
Feeding habit	Deposit feeder	0	-0.046	-0.139	0	0
Feeding habit	Shredder	0	0	0	-0.008	0.128
Feeding habit	Scraper	-0.012	0	-0.043	0	0
Feeding habit	Filter feeder	0.068	0	0.050	0.046	0
Feeding habit	Predator	-0.030	0	-0.044	-0.036	-0.023
Substratum preference	Boulders, cobbles	0	-0.009	0.033	-0.084	0
Substratum preference	Gravel	0	0	0.034	0.122	0.022
Substratum preference	Sand	0.065	0	0.060	-0.043	-0.167
Substratum preference	Macrophytes	0	0.262	0.050	0	-0.216
Substratum preference	Twigs, roots	-0.049	0.080	0	0	-0.158
Substratum preference	Detritus, litter	0	0	0	-0.052	0
Substratum preference	Mud	0	0.148	0.142	0	-0.050

et al. (2015) who consider regional complexity to be a crucial factor in guiding the selection of both restoration measures and natural reference conditions.

The relevance of ecoregion and catchment size was also confirmed in the multivariate modeling approach, but with no evidence of an interactive effect of ecoregion, catchment size and restoration age. Likewise, the selected species traits were hardly able to explain the variability of species responses to a growing restoration age. Filter feeders and sand dwelling taxa appeared to have benefitted slightly from growing restoration ages, whereas dead-wood dwelling taxa decreased in turn. Yet, due to weak model goodness and rather modest coefficients, these results should not be over-interpreted. Regardless of the gradient in restoration age, the model outcomes tended to reflect that taxa dwelling on macrophytes or fine particulate matter benefitted from lowland conditions (i.e., reduced slopes and flow velocities) and were tolerant against conditions following intensive land use (e.g., increased input of fine sediments). For taxa with small body sizes and high dispersal abilities, an increased positive correlation was observed between the taxon's abundance in the restored sections and the biotic integrity of the corresponding control sections (MMI_control), which can be seen as a proxy variable for the condition of the source populations. In accordance with other recent studies (Li et al., 2015, Sundermann et al., 2011 and Tonkin et al., 2014), this might indicate that recolonization of the restored sections is originating from source populations in the proximity and is primarily driven by good dispersers.

4.4. Limitations of our approach

The lack of prior restoration data is a very common issue in restoration ecology sciences, as status quo assessments and integrated monitoring programs are rarely part of the restoration planning. Assessments of restoration success are therefore often restricted to pairwise comparisons of restored versus non-restored 'control' sites (as we have done here), taking spatial differences as surrogates for temporal changes (space-for-time substitution approach). This study design has some disadvantages to be aware of; the most important one being the impossibility of accounting for inherent variability over time (Pickett, 1989; Thomaz et al., 2012). Specifically, control site conditions might have changed since restoration (e.g., in water quality, hydromorphology, hydrology and community patterns). Careful selection of the sites must therefore ensure comparability in spite of possible changes over time. This gives weight to the need of sampling prior to restoration, which would enable a true Before-After-Control-Impact design.

Finally, we stress that the precision of freshwater biological sampling results would highly benefit from replicated samplings, as sampling variation is typically high in lotic systems (Clarke et al., 2006). However, given the high effort associated with replicated samplings, a lack of replicates is a common flaw in applied ecological field studies and basically a matter of a lack in feasibility.

5. Conclusion

In the present study, we assessed the importance of the time since restoration (i.e., restoration age) and other factors (e.g., catchment characteristics) in explaining benthic invertebrate community change in response to hydromorphological river restoration.

As implied by our hypotheses, we found evidence for both community disturbance and recovery following the restoration event. However, the restoration age was only a weak predictor of community integrity and responses were strongly overridden by catchment-scale factors. Our results suggest that local structural improvements alone were still insufficient either in quantity or quality or both. We conclude that the lack of time is not the ultimate reason for missing community recovery and the problem is more likely within the restoration design and the missing ability to cure catchment-wide symptoms with reconstructing channels locally.

From an ecological point of view, future river restoration will benefit from re-establishing near-natural water quality conditions and catchment-scale processes (e.g., connectivity and hydrodynamics) in parallel to restoring local habitat structure (Roni et al., 2008). For instance, installing riparian buffer strips and promoting highly efficient waste water treatment plants could help mitigating the influence of intensive land use and urbanization. Dam removal is essential for reconnecting isolated river reaches and for improving the hydrological regime. However, as shown in Leps et al. (2015), the measures needed may also differ between stream types. This highlights the importance of recognizing the inherent heterogeneity of riverscapes when tackling such applied issues.

According to a recent study of Jähnig et al. (2011), socioeconomic aspects of river restoration should not be disregarded. The citizens' perception of river restoration success is based on a variety of additional factors such as the recreational value and landscape aesthetic values, which clearly benefited from river restoration (Jähnig et al., 2011). Public opinion surveys have shown that river restoration receives a high level of acceptance and support in the public, although expenditures are well known to be high (Deffner et al., in preparation). River restoration may therefore be ideal to promote the citizens' awareness of both the need and value of intact river ecosystems. Finally, river restoration will help to increase the public acceptance for future efforts in enhancing the water quality and improving riverine communities, even if most of these changes may occur unseen.

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.scitotenv.2016.03.120.

Acknowledgments

This work was financially supported by German Federal Environmental Foundation (Deutsche Bundesstiftung Umwelt; AZ 31007 – 33/2), Kurt Lange Foundation (Kurt-Lange-Stiftung), Hessian Foundation for Nature Conservation (Stiftung Hessischer Naturschutz; AZ: SHN 1059), Kreissparkasse Foundation Gelnhausen (Stiftung Kreissparkasse Gelnhausen) and by the EU-funded Integrated Project REFORM (Restoring rivers for effective catchment Management; EU FP 7, Grant Agreement No. 282656).

References

Allan, J.D., 2004. Landscapes and riverscapes: the influence of land use on stream ecosystems. Annu. Rev. Ecol. Syst. 35, 257–284. http://dx.doi.org/10.1146/annurev.ecolsys.35.120202.110122.

Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecol. 26, 32–46. http://dx.doi.org/10.1111/j.1442-9993.2001.01070.pp.x.

Armitage, P., Moss, D., Wright, J., Furse, M., 1983. The performance of a new biological water quality score system based on macroinvertebrates over a wide range of unpolluted running-water sites. Water Res. 17, 333–347. http://dx.doi.org/10.1016/0043-1354(83)90188-4.

Banning, M., 1998. Auswirkungen des Aufstaus größerer Flüsse auf das Makrozoobenthos, dargestellt am Beispiel der Donau. Essener ökologische Schriften 9. Westarp-Wiss, Hohenwarsleben.

Barbour, M. T.; Gerritsen, J.; Snyder B.D.; Stribling, J. B., 1999. Rapid Bioassessment Protocols for Use in Streams and Wadeable Rivers: Periphyton, Benthic Macroinvertebrates and Fish, second edition. EPA 841-B-99-002. Washington, D.C.: U.S. Environmental Protection Agency; Office of Water.

Bash, J.S., Ryan, C.M., 2002. Stream restoration and enhancement projects: is anyone monitoring? Environ. Manag. 29, 877–885. http://dx.doi.org/10.1007/s00267-001-0066-3.

Baxter, C.V., Fausch, K.D., Saunders, W.C., 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. Freshw. Biol. 50, 201–220. http://dx.doi.org/10.1111/j.1365-2427.2004.01328.x.

Bernhardt, E.S., Palmer, M.A., 2011. River restoration: the fuzzy logic of repairing reaches to reverse catchment scale degradation. Ecol. Appl. 21, 1926–1931.

Bernhardt, E.S., Palmer, M.A., Allan, J.D., Alexander, G., Barnas, K., et al., 2005. Ecology. Synthesizing U.S. river restoration efforts. Science 308, 636–637. http://dx.doi.org/10.1126/science.1109769.

Biggs, J., Corfield, A., Gron, P., Hansen, H.O., Walker, D., et al., 1998. Restoration of the rivers Brede, Cole and Skerne: a joint Danish and British EU-LIFE demonstration project, V-short-term impacts on the conservation value of aquatic macroinvertebrate and macrophyte assemblages. Aquat. Conserv. 8 (1), 241–255.

Böhmer, J., Rawer-Jost, C., Zenker, A., Meier, C., Feld, C.K., et al., 2004. Assessing streams in Germany with benthic invertebrates: development of a multimetric invertebrate based assessment system. Limnologica 34, 416–432. http://dx.doi.org/10.1016/S0075-9511(04)80010-0.

Brown, A.M., Warton, D.I., Andrew, N.R., Binns, M., Cassis, G., et al., 2014. The fourth-corner solution - using predictive models to understand how species traits interact with the environment. Methods Ecol. Evol. 5, 344–352. http://dx.doi.org/10.1111/2041-210X.12163.

Clarke, K.R., Ainsworth, M., 1993. A method of linking multivariate community structure to environmental variables. Mar. Ecol. Prog. Ser. 92, 205–219. http://dx.doi.org/10.3354/meps092205.

Clarke, R.T., Lorenz, A.W., Sandin, L., Schmidt-Kloiber, A., Strackbein, J., et al., 2006. Effects of sampling and sub-sampling variation using the STAR-AQEM sampling protocol on the precision of macroinvertebrate metrics. Hydrobiologia 566, 441–459. http://dx.doi.org/10.1007/s10750-006-0078-3.

Cohen, J., 1988. Statistical Power Analysis for the Behavioral Sciences. second ed. Lawrence Earlbaum Associates, Hillsdale, NJ.

Davies-Colley, R.J., Meleason, M.A., Hall, R.M., Rutherford, J.C., 2009. Modelling the time course of shade, temperature, and wood recovery in streams with riparian forest restoration. N. Z. J. Mar. Freshw. Res. 43, 673–688. http://dx.doi.org/10.1080/00288330909510033.

Death, R.G., Zimmermann, E.M., 2005. Interaction between disturbance and primary productivity in determining stream invertebrate diversity. Oikos 111, 392–402. http://dx.doi.org/10.1111/j.0030-1299.2005.13799.x.

Deffner, J., Birzle-Hader, B., Haase, P., 2016. Beyond the Eu Water Framework Directive: Societal Relevance of River Restoration in preparation.

Doll, B.A., Jennings, G.D., Spooner, J., Penrose, D.L., Usset, J.L., 2015. Evaluating the eco-geomorphological condition of restored streams using visual assessment and macroinvertebrate metrics. J. Am. Water Resour. As. 51, 68–83. http://dx.doi.org/10.1111/jawr.12233.

Domisch, S., Jähnig, S.C., Haase, P., 2011. Climate-change winners and losers: stream macroinvertebrates of a submontane region in Central Europe. Freshw. Biol. 56, 2009–2020. http://dx.doi.org/10.1111/j.1365-2427.2011.02631.x.

Dufour, S., Piégay, H., 2009. From the myth of a lost paradise to targeted river restoration: forget natural references and focus on human benefits. River Res. Appl. 25, 568–581. http://dx.doi.org/10.1002/rra.1239.

EU Commission, 2000. Directive 2000/60/EC of the European Parliament and of the Council of 23th October 2000 establishing a framework for the community action in the field of water policy. Off. J. Eur. Union 237, 1–72.

Friedrich, G., Herbst, V., 2004. Eine erneute Revision des Saprobiensystems - weshalb und wozu? Acta Hydrochim. Hydrobiol. 32, 61–74. http://dx.doi.org/10.1002/aheh.200300518.

Fuchs, U., Statzner, B., 1990. Time scales for the recovery potential of river communities after restoration: lessons to be learned from smaller streams. Regul. River. 5, 77–87. http://dx.doi.org/10.1002/rrr.3450050108.

Gore, J.A., Milner, A.M., 1990. Island biogeographical theory: can it be used to predict lotic recovery rates? Environ. Manag. 14, 737–753. http://dx.doi.org/10.1007/BF02394722.

Gustafsson, S., Österling, M., Skurdal, J., Schneider, L.D., Calles, O., 2013. Macroinvertebrate colonization of a nature-like fishway: the effects of adding habitat heterogeneity. Ecol. Eng. 61, 345–353. http://dx.doi.org/10.1016/j.ecoleng.2013.09.023.

Haase, P., Hering, D., Jähnig, S.C., Lorenz, A.W., Sundermann, A., 2013. The impact of hydromorphological restoration on river ecological status: a comparison of fish, benthic invertebrates, and macrophytes. Hydrobiologia 704, 475–488. http://dx.doi.org/10.1007/s10750-012-1255-1.

Haase, P., Lohse, S., Pauls, S., Schindehütte, K., Sundermann, A., et al., 2004. Assessing streams in Germany with benthic invertebrates: development of a practical standardised protocol for macroinvertebrate sampling and sorting. Limnologica 34, 349–365. http://dx.doi.org/10.1016/S0075-9511(04)80005-7.

Haase, P., Schindehütte, K., Sundermann, A., 2006. Operationelle Taxaliste als Mindestanforderung an die Bestimmung von Makrozoobenthosproben aus Fließgewässern zur Umsetzung der EU-Wasserrahmenrichtlinie in Deutschland. http://www.fliessgewaesserbewertung.de/download/bestimmung accessed 30.09.15.

Harding, J.S., Benfield, E.F., Bolstad, P.V., Helfman, G.S., Jones, E.B.D., 1998. Stream biodiversity: the ghost of land use past. P. Natl. Acad. Sci. 95, 14843–14847. http://dx.doi.org/10.1073/pnas.95.25.14843.

Hering, D., Buffagni, A., Moog, O., Sandin, L., Sommerhäuser, M., et al., 2003. The development of a system to assess the ecological quality of streams based on macroinvertebrates – design of the sampling programme within the AQEM Project. Int. Rev. Hydrobiol. 88, 345–361. http://dx.doi.org/10.1002/iroh.200390030.

Hering, D., Meier, C., Rawer-Jost, C., Feld, C.K., Biss, R., et al., 2004a. Assessing streams in Germany with benthic invertebrates: selection of candidate metrics. Limnologica 34, 398–415. http://dx.doi.org/10.1016/S0075-9511(04)80009-4.

Hering, D., Moog, O., Sandin, L., Verdonschot, P.F., 2004b. Overview and application of the AQEM assessment system. Hydrobiologia 516, 1–20. http://dx.doi.org/10.1023/B:HYDR.0000025255.70009.a5.

Howard-Williams, C., Pickmere, S., 1994. Long-term vegetation and water quality changes associated with the restoration of a pasture stream. In: Collier, K.J. (Ed.), Restoration of Aquatic Habitats. Selected Papers From the Second Day of the New Zealand Limnological Society 1993 Annual Conference, 10–12 May 1993, Wellington, New Zealand. Dept. of Conservation, Wellington, N.Z., pp. 93–109.

Jähnig, S.C., Lorenz, A., Hering, D., 2008. Hydromorphological parameters indicating differences between single- and multiple-channel mountain rivers in Germany, in relation to their modification and recovery. Aquat. Conserv. 18, 1200–1216. http://dx.doi.org/10.1002/aqc.875.

Jähnig, S.C., Lorenz, A.W., Hering, D., Antons, C., Sundermann, A., et al., 2011. River restoration success: a question of perception. Ecol. Appl. 21, 2007–2015.

Januschke, K., Jähnig, S.C., Lorenz, A.W., Hering, D., 2014. Mountain river restoration measures and their success(ion): effects on river morphology, local species pool, and functional composition of three organism groups. Ecol. Indic. 38, 243–255. http://dx.doi.org/10.1016/j.ecolind.2013.10.031.

Jones, H.P., Schmitz, O.J., 2009. Rapid recovery of damaged ecosystems. PLoS One 4, e5653. http://dx.doi.org/10.1371/journal.pone.0005653.

Kamp, U., Binder, W., Hölzl, K., 2007. River habitat monitoring and assessment in Germany. Environ. Monit. Assess. 127, 209–226. http://dx.doi.org/10.1007/s10661-006-9274-x.

Kappes, H., Haase, P., 2012. Slow, but steady: dispersal of freshwater molluscs. Aquat. Sci. 74, 1–14. http://dx.doi.org/10.1007/s00027-011-0187-6.

Keil, M., Bock, M., Esch, T., Metz, A., Nieland, S., Pfitzner, A., 2010. CORINE Land Cover Aktualisierung 2006 für Deutschland. Abschlussbericht zu den F + E Vorhaben UBA FKZ 3707 12 200 und FKZ 3708 12 200. Deutsches Zentrum für Luft- und Raumfahrt e.V., Deutsches Fernerkundungsdatenzentrum Oberpfaffenhofen.

Laasonen, P., Muotka, T., Kivijärvi, I., 1998. Recovery of macroinvertebrate communities from stream habitat restoration. Aquat. Conserv. 8, 101–113. http://dx.doi.org/10.1002/(SICI)1099-0755(199801/02)8:1<101::AID-AQC251>3.0.CO;2-4.

Lake, P.S., Bond, N., Reich, P., 2007. Linking ecological theory with stream restoration. Freshw. Biol. 52, 597–615. http://dx.doi.org/10.1111/j.1365-2427.2006.01709.x.

Langford, T., Shaw, P.J., Ferguson, A., Howard, S.R., 2009. Long-term recovery of macroinvertebrate biota in grossly polluted streams: re-colonisation as a constraint to ecological quality. Ecol. Indic. 9, 1064–1077. http://dx.doi.org/10.1016/j.ecolind.2008.12.012.

Larson, S.J., Gilliom, R.J., Capel, P.D., 1999. Pesticides in Streams of the United States—Initial Results From the National Water-Quality Assessment Program. US Geological Survey Water-Resources Investigations Report. pp. 98–4222 California.

Lave, R., 2009. The controversy over natural channel design: substantive explanations and potential avenues for resolution. J. Am. Water Resour. As. 45, 1519–1532. http://dx.doi.org/10.1111/j.1752-1688.2009.00385.x.

Legendre, P., Legendre, L., 1998. Numerical Ecology. 2nd English ed. Elsevier.

Leps, M., Tonkin, J.D., Dahm, V., Haase, P., Sundermann, A., 2015. Disentangling environmental drivers of benthic invertebrate assemblages: the role of spatial scale and riverscape heterogeneity in a multiple stressor environment. Sci. Total Environ. 536, 546–556. http://dx.doi.org/10.1016/j.scitotenv.2015.07.083.

Li, F., Sundermann, A., Stoll, S., Haase, P., 2015. A newly developed dispersal capacity metric indicates succession of benthic invertebrates in restored rivers. PeerJ PrePrints 3, e1125. http://dx.doi.org/10.7287/peerj.preprints.911v1.

Lorenz, A.W., Hering, D., Feld, C.K., Rolauffs, P., 2004. A new method for assessing the impact of hydromorphological degradation on the macroinvertebrate fauna of five German stream types. Hydrobiologia 516, 107–127. http://dx.doi.org/10.1023/B:HYDR.0000025261.79761.b3.

Lorenz, A.W., Jähnig, S.C., Hering, D., 2009. Re-meandering German lowland streams: qualitative and quantitative effects of restoration measures on hydromorphology and macroinvertebrates. Environ. Manag. 44, 745–754. http://dx.doi.org/10.1007/s00267-009-9350-4.

Louhi, P., Mykrä, H., Paavola, R., Huusko, A., Vehanen, T., et al., 2011. Twenty years of stream restoration in Finland: little response by benthic macroinvertebrate communities. Ecol. Appl. 21, 1950–1961.

McFadden, D., 1974. Conditional Logit Analysis of Qualitative Choice Behavior. Academic Press, Frontiers of Econometrics. New York, pp. 105–142.

McMillan, S.K., Tuttle, A.K., Jennings, G.D., Gardner, A., 2014. Influence of restoration age and riparian vegetation on reach-scale nutrient retention in restored urban streams. J. Am. Water Resour. As. 50, 626–638. http://dx.doi.org/10.1111/jawr.12205.

Meli, P., Benayas, Rey, María, José, Balvanera, P., Martínez Ramos, M., 2014. Restoration enhances wetland biodiversity and ecosystem service supply, but results are context-dependent: a meta-analysis. PLoS One 9, e93507. http://dx.doi.org/10.1371/journal.pone.0093507.

Miller, S.W., Budy, P., Schmidt, J.C., 2010. Quantifying macroinvertebrate responses to in-stream habitat restoration: applications of meta-analysis to river restoration. Restor. Ecol. 18, 8–19. http://dx.doi.org/10.1111/j.1526-100X.2009.00605.x.

Nienhuis, P.H., Leuven, R., 2001. River restoration and flood protection: controversy or synergism? Hydrobiologia 444, 85–99. http://dx.doi.org/10.1023/A:1017509410951.

Nilsson, C., Polvi, L.E., Gardeström, J., Hasselquist, E.M., Lind, L., et al., 2015. Riparian and in-stream restoration of boreal streams and rivers: success or failure? Ecohydrology 8, 753–764. http://dx.doi.org/10.1002/eco.1480.

Oksanen, J., Guillaume Blanchet, F., Kindt, R., Legendre, P., Minchin, P.R., et al., 2015. Package 'vegan'. Community Ecology Package for R https://cran.r-project.org/web/packages/vegan/vegan.pdf accessed 15.07.2015.

Ormerod, S.J., 2004. A golden age of river restoration science? Aquat. Conserv. 14, 543–549. http://dx.doi.org/10.1002/aqc.663.

Palmer, M.A., Menninger, H.L., Bernhardt, E., 2010. River restoration, habitat heterogeneity and biodiversity: a failure of theory or practice? Freshw. Biol. 55, 205–222. http://dx.doi.org/10.1111/j.1365-2427.2009.02372.x.

Pasquale, N., Perona, P., Schneider, P., Shrestha, J., Wombacher, A., et al., 2011. Modern comprehensive approach to monitor the morphodynamic evolution of a restored river corridor. Hydrol. Earth Syst. Sc. 15, 1197–1212. http://dx.doi.org/10.5194/hess-15-1197-2011.

Pickett, S.T.A., 1989. Space-for-time substitution as an alternative to long-term studies. In: Likens, G.E. (Ed.), Long-Term Studies in Ecology, Approaches and Alternatives. Springer, New York http://dx.doi.org/10.1007/978-1-4615-7358-6_5.

Pielou, E.C., 1966. The measurement of diversity in different types of biological collections. J. Theor. Biol. 13, 131–144. http://dx.doi.org/10.1016/0022-5193(66)90013-0.

Core Team, R., 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austriahttp://www.R-project.org accessed 30.09.2015.

Robertson, A., Dineen, G., Baker, R., Hancock, B., Shaw, P., 2014. Microinvertebrate community colonisation and succession in a new urban river: lessons for river restoration. Fundam. Appl. Limnol. 185, 31–41. http://dx.doi.org/10.1127/fal/2014/0615.

Rolauffs, P., Stubauer, I., Zahrádková, S., Brabec, K., Moog, O., 2004. Integration of the saprobic system into the European Union Water Framework Directive – case studies in Austria, Germany and Czech Republic. Hydrobiologia 516, 285–298. http://dx.doi.org/10.1023/B:HYDR.0000025271.90133.4d.

Roni, P., Hanson, K., Beechie, T., 2008. Global review of the physical and biological effectiveness of stream habitat rehabilitation techniques. N. Am. J. Fish Manag. 28, 856–890. http://dx.doi.org/10.1577/M06-169.1.

Rosgen, D.L., 2011. Natural channel design: fundamental concepts, assumptions, and method. In: A. Simon, S. J. Bennett und J. M. Castro: Stream Restoration in Dynamic Fluvial Systems. Washington D.C.: American Geophysical Union (Geophysical Monograph Series), 69–93.

Sarr, D.A., 2002. Riparian livestock exclosure research in the Western United States: a critique and some recommendations. Environ. Manag. 30, 516–526. http://dx.doi.org/10.1007/s00267-002-2608-8.

Shannon, C.E., 1948. A mathematical theory of communication. AT&T Tech. J. 27, 623–656. http://dx.doi.org/10.1002/j.1538-7305.1948.tb00917.x.

Simpson, E.H., 1949. Measurement of diversity. Nature 163, 688. http://dx.doi.org/10.1038/163688a0.

Spänhoff, B., Arle, J., 2007. Setting attainable goals of stream habitat restoration from a macroinvertebrate view. Restor. Ecol. 15, 317–320. http://dx.doi.org/10.1111/j.1526-100X.2007.00216.x.

Sponseller, R.A., Benfield, E.F., Valett, H.M., 2001. Relationships between land use, spatial scale and stream macroinvertebrate communities. Freshw. Biol. 46, 1409–1424. http://dx.doi.org/10.1046/j.1365-2427.2001.00758.x.

Stoll, S., Breyer, P., Tonkin, J.D., Früh, D., Haase, P., 2016. Scale-dependent effects of river habitat quality on benthic invertebrate communities — implications for stream restoration practice. Sci. Total Environ. 553, 495–503. http://dx.doi.org/10.1016/j.scitotenv.2016.02.126.

Sundermann, A., Gerhardt, M., Kappes, H., Haase, P., 2013. Stressor prioritisation in riverine ecosystems: which environmental factors shape benthic invertebrate assemblage metrics? Ecol. Indic. 27, 83–96. http://dx.doi.org/10.1016/j.ecolind.2012.12.003.

Sundermann, A., Stoll, S., Haase, P., 2011. River restoration success depends on the species pool of the immediate surroundings. Ecol. Appl. 21, 1962–1971.

Sweeney, B.W., Bott, T.L., Jackson, J.K., Kaplan, L.A., Newbold, J.D., et al., 2004. Riparian deforestation, stream narrowing, and loss of stream ecosystem services. P. Natl. Acad. Sci. 101, 14132–14137. http://dx.doi.org/10.1073/pnas.0405895101.

Therneau, T.M., Atkinson, B., Ripley, B., 2015. Package 'rpart', Recursive Partitioning For Classification, Regression and Survival Trees, Package for R. https://cran.r-project.org/web/packages/rpart/rpart.pdf accessed 15.07.2015.

Therneau, T.M., Atkinson, E.J., 1997. An introduction to recursive partitioning using the RPART routines. Tech. Rep.Mayo Foundation

Thomaz, S.M., Agostinho, A.A., Gomes, L.C., Silveira, M.J., Rejmanek, M., et al., 2012. Using space-for-time substitution and time sequence approaches in invasion ecology. Freshw. Biol. 57, 2401–2410. http://dx.doi.org/10.1111/fwb.12005.

Tibshirani, R., 2011. Regression shrinkage and selection via the lasso: a retrospective. J. Roy. Stat. Soc. B Met. 73 (3), 273–282. http://dx.doi.org/10.1111/j.1467-9868.2011.00771.x.

Tonkin, J.D., Death, R.G., 2012. Consistent effects of productivity and disturbance on diversity between landscapes. Ecology 3, art108. DOI: http://dx.doi.org/10.1890/ES12-00243.1.

Tonkin, J.D., Stoll, S., Sundermann, A., Haase, P., 2014. Dispersal distance and the pool of taxa, but not barriers, determine the colonisation of restored river reaches by benthic invertebrates. Freshw. Biol. 59, 1843–1855. http://dx.doi.org/10.1111/fwb.12387.

Townsend, C.R., Uhlmann, S.S., Matthaei, C.D., 2008. Individual and combined responses of stream ecosystems to multiple stressors. J. Appl. Ecol. 45, 1810–1819. http://dx.doi.org/10.1111/j.1365-2664.2008.01548.x.

Tullos, D.D., Penrose, D.L., Jennings, G.D., Cope, W.G., 2009. Analysis of functional traits in reconfigured channels: implications for the bioassessment and disturbance of river restoration. J. N. Am. Benthol. Soc. 28, 80–92. http://dx.doi.org/10.1899/07-122.1.

Wagenhoff, A., Townsend, C.R., Phillips, N., Matthaei, C.D., 2011. Subsidy-stress and multiple-stressor effects along gradients of deposited fine sediment and dissolved nutrients in a regional set of streams and rivers. Freshw. Biol. 56, 1916–1936. http://dx.doi.org/10.1111/j.1365-2427.2011.02619.x.

Wang, Y., Naumann, U., Wright, S., Warton, D., 2015. Package 'mvabund', Statistical Methods for Analysing Multivariate Abundance Data, package for R. https://cran.r-project.org/web/packages/mvabund/mvabund.pdf accessed 28.07.2015.

Wang, Y., Naumann, U., Wright, S.T., Warton, D.I., 2012. mvabund - an R package for model-based analysis of multivariate abundance data. Methods Ecol. Evol. 3, 471–474. http://dx.doi.org/10.1111/j.2041-210X.2012.00190.x.

Ward, J.V., Tockner, K., Arscott, D.B., Claret, C., 2002. Riverine landscape diversity. Freshw. Biol. 47, 517–539. http://dx.doi.org/10.1046/j.1365-2427.2002.00893.x.

Wilcoxon, F., 1945. Individual comparisons by ranking methods. Biol. Bull. 1, 80–83. http://dx.doi.org/10.2307/3001968.

Winking, C., Lorenz, A.W., Sures, B., Hering, D., 2014. Recolonisation patterns of benthic invertebrates: a field investigation of restored former sewage channels. Freshw. Biol. 59, 1932–1944. http://dx.doi.org/10.1111/fwb.12397.

Woolsey, S., Capelli, F., Gonser, T.O., Hoehn, E., Hostmann, M., et al., 2007. A strategy to assess river restoration success. Freshw. Biol. 52, 752–769. http://dx.doi.org/10.1111/j.1365-2427.2007.01740.x.