Response of fish species to river restoration – the role of species traits

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Abstract

Species are known to respond differently to restoration efforts, but we still lack a clear conceptual understanding of these differences. We analyzed the development of an entire fish community as well as the relationship between multi-metric response patterns of fish species and their ecological species traits at a comprehensively monitored river restoration project, the Lippe River in Germany. Using electrofishing data from 21 consecutive years (4 years pre- and 17 years post-restoration) from multiple restored and unrestored control reaches, we demonstrated that this restoration fully reached its targets, approximately doubling both species richness and abundance. Species richness continuously increased while fish density exhibited an overshooting response in the first years post restoration. Both richness and abundances stabilized approximately seven years after the restoration, although interannual variability remained considerable. The response of each species to the restoration was characterized using a set of six parameters. Relating the dissimilarity in species response to their ecological dissimilarity, based on 13 species traits, we found life-history and reproduction-related traits were the most important for species' responses to restoration. Short-lived species with early female maturity and multiple spawning runs per year exhibited the strongest response, reflecting the ability of fast reproducers to rapidly colonize new habitats. Fusiform-bodied species also responded more positively than deep-bodied species, reflecting the success of this restoration to reform appropriate hydromorphological conditions (riffles and shallow bays), for which these species depend. Our results demonstrate that repeated sampling over periods longer than seven years are necessary to reliably assess river restoration outcomes. Furthermore, this study emphasizes the utility of species traits for examining restoration outcomes, particularly the metapopulation and metacommunity processes driving recovery dynamics. Focusing on species traits instead of species identity also allows for easier transfer of knowledge to other biogeographic areas and promotes coupling to functional ecology.

Introduction

River restoration, as requested by the European Water Framework Directive (European EC 2000) and other similar legislation worldwide, aims to return rivers to natural or near-natural conditions. Restoration projects, therefore, not only focus on individual species but entire river communities, together with the underlying natural structures and processes that support them. The traditional approach of river restoration has been to mitigate the shortcomings in hydromorphological and physico-chemical conditions, with the hope of communities tracking these changes (Palmer et al. 1997). A number of comparative analyses have been published recently showing that these types of restoration have highly variable results; some studies found positive effects of restoration on species abundances and richness (Kail et al. 2015; Thomas et al. 2015; Whiteway et al. 2010), while others found no clear effects (Haase et al. 2013; Nilsson et al. 2014; Schmutz et al. 2016; Sundermann et al. 2011).

This variability likely reflects several different factors, such as: 1. Differences in the effectiveness of the individual sets of restoration measures applied (Roni et al. 2008; Simaika et al. 2015). 2. Different catchment-scale characteristics that may override local habitat restoration (Bernhardt & Palmer 2011). 3. Limitations in the regional species pool, with several recent studies demonstrating its importance for the colonization of restored reaches for both fish and macroinvertebrates (Stoll et al. 2014; Stoll et al. 2013; Sundermann et al. 2011; Tonkin et al. 2014). Yet, even taking into consideration occurrence rates and densities of fish species in the surrounding reaches that serve as source populations, certain species may more readily colonize restored reaches than others (Stoll et al. 2013).

The underlying patterns and processes that drive outcomes of restorations are not well understood. For this reason, Bernhardt et al. (2011) called to shift the focus of restoration research from documenting success or failure to understanding the causes of success or failure. By drawing more readily on ecological theory (Lake et al. 2007), in turn developing a better theoretical understanding of the ongoing processes at restored reaches, research will better inform future restoration approaches through identifying generalizable patterns. In this respect species traits might provide a helpful tool in analyzing succession processes. Recent studies have already used individual species traits or limited sets of few species traits as co-variables to explain restoration outcomes. For example, Li et al. (2015) showed that dispersal capacity of benthic invertebrate species drives the community dynamics at restored sites. Lorenz et al. (2013) showed that reproductive guilds of fish profited differently from restorations. Yet, the attention has rarely been directed on a broad spectrum of species traits even though they are expected to play an important role in the process of habitat colonization (Stoll et al. 2014). Here, we focused on four trait types, which relate to species characteristics that are potentially important in the context of colonization of a restored reach. The first type was related to body morphology and dispersal. It has been shown in a range of studies, that dispersal distance is a limiting factor in the colonization process of restored reaches, both for macroinvertebrates (Sundermann et al. 2011; Tonkin et al. 2014) and fish (Stoll et al. 2014; Stoll et al. 2013) and the dispersal distance was shown to relate to morphological traits (e.g. body size; Radinger & Wolter 2014). The second type of traits related to foraging, which is potentially relevant as food webs need to establish at restored reaches, with complex intra- and interspecific dynamics in feeding guilds. The third type focused on habitat use, as restorations remodel habitat structures, creating new habitats and diminishing others. Finally, the fourth set of traits related to reproduction and life-table characteristics, which describe the ability to establish and maintain different levels of propagule pressure to facilitate colonization and build up populations at restored reaches (Stoll et al. 2016). Life-history strategies determine the pace in which species are able to respond to variation in environmental properties.

To gain such a functional understanding of the community processes in restored rivers, high-intensity monitoring of entire communities pre- and post-restoration are necessary and as monitoring is costly, appropriate datasets are rare. If monitoring is carried out at all, it is mostly limited to a singular before-after or treatment-control comparison. Due to this lack of real time series, there is still considerable uncertainty on the speed of the recolonization processes at restored river reaches. Some restorations are evaluated as early as half a year after completion of the restoration while others have only been monitored after 19 years (Thomas et al. 2015). A range of studies have detected temporal effects on the perceived restoration outcomes. Some studies highlighted a positive correlation between the probability of species detection at restored reaches and time since restoration (Stoll et al. 2014; Tonkin et al. 2014), while others point to a long-term decrease in restoration effect (Kail et al. 2015) and a return to community composition of unrestored conditions (Thomas et al. 2015). Given such variability, inconsistent sample timing clearly adds to the variation of reported restoration outcomes.

To address these questions, we analyzed multi-metric species response patterns to restoration in relation to their species traits and we aggregate these species responses to evaluate the changes in the entire community over the monitoring period. In doing so, we addressed the following questions: 1) How fast did the fish community develop into a stable state that allows a final evaluation of a restoration’s outcome. 2) Which species traits allow species to respond favourably to restoration?

We used fish community data from an intensively monitored restoration project at the Lippe River, Germany. Data comprised four consecutive years of pre- and 17 years of post-restoration from multiple sections in the restored and unrestored control reaches.

The answers to these questions will improve our general understanding of fish species and community response patterns to river restoration and can be used to improve both restoration approaches and monitoring regimes. Focusing our analyses on species traits instead of taxonomic identities, the results provide a better insight in ecological functioning and are more easily transferable to other biogeographic regions.

Materials and Methods

Description of restoration project study site

We investigated a river restoration project situated in the Lippe River, a tributary to the Rhine River in North Rhine-Westphalia, Germany. From the year 1815 onwards, the hydromorphological structure of the Lippe River was altered by the construction of water gates near mills, channelization and fixation of river banks, profile constriction and deepening, shortening of the river course by cutting off meanders, removal of marl barriers, removal of deadwood, clearing shrubs and trees close to the shore and floodplain drainage for agriculture lead to lateral erosion and incision (ABU 2010, 2013). Despite not being a major waterway, by 1990, the river banks were completely fixed and the Lippe River had lost approximately one fifth of its original length (ABU 2010, 2013).

In 1990, the German federal state North Rhine-Westphalia introduced a floodplain restoration program with the general objective to create dynamic rivers and floodplains that would develop, if possible, without further human interference upon completion of restoration projects (ABU 2010). Such a restoration project has been executed and monitored since then by the biological station “Arbeitsgemeinschaft Biologischer Umweltschutz im Kreis Soest e.V.” (ABU).

This first reach-scale river restoration project at the Lippe River was implemented by the District Council of Arnsberg in 1996 and 1997 at Klostermersch close to Benninghausen, embracing approximately an area of 1.3 km² and a river reach of about 2,000 m (Fig. 1). To re-establish and connect the river’s floodplain with the river, extensive restoration actions were carried out: bank fixations were removed, the river was widened from about 18 m to 45 m, and the river bed was lifted by approximately 2 m (Fig. 1, ABU 2010). A series of oxbows and some small islands were built, and full-grown trees were introduced as deadwood. The drainage of the floodplain was stopped, and a number of flood channels and temporary standing water pools in the floodplain area were created. Finally, a number of rare plant species (e.g. *Butomus umbellatus*) were transplanted (ABU 2010; Detering 2008).

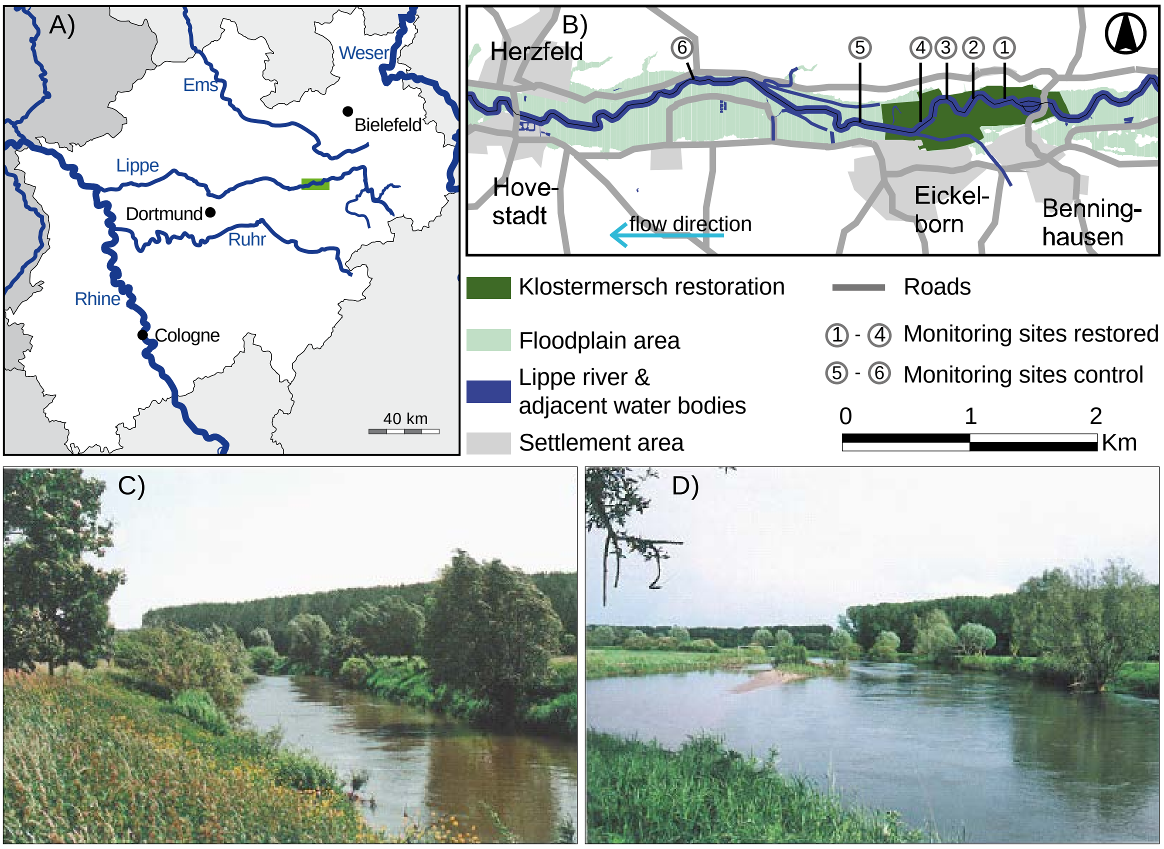

Figure 1: Overview of the restoration project. (A) Location of the Lippe River and the restoration project area (green rectangle) within the German State of North Rhine-Westphalia. (B) Detailed map of the Klostermersch (KM) restoration reach and the six sampling sites. (C) Photo of the KM area before restoration with a relatively straight river that is carved deeply in its bed and has no contact to the riparian meadows, and (D) KM after restoration, where the river is in contact with meadows due to a bottom-lift of the river bed, and the habitat spectrum is widened, such as by creation of sand banks and still water areas. Photos by courtesy of J. Drüke.

The restoration project resulted in a naturally dynamic development of the hydromorphology of the Lippe River. For instance, substrate material is now translocated by major floods, river banks erode, the current velocity determines river bed composition, and the river floods into the floodplain on at least an annual basis; all aspects not present in its channelized form (ABU

2010). Therefore, from a hydromorphological perspective, the restoration project is considered successful.

Survey of the fish community at the restored and the unrestored control reaches

Boat electrofishing was carried out annually by the ABU between 1993 and 2013 (four years prior to restoration, 17 years post restoration) to monitor fish communities at the restored and unrestored reaches. Fishing was conducted at four sites (total length 635 m) within the restored river reach and at two unrestored control sites (total length 320 m) nearby, downstream of the restored reach (Fig. 1). The hydromorphological structure of the control sites closely resembles unrestored conditions at the restored reach. Such detailed, long-term monitoring data from a river restoration project following the full BACI (before-after-control-impact) design are very rare. Sampling was carried out in August or September at stable low discharge with high water transparency. Due to extreme floods sampling was not possible at two of four sites (L1 and L2; Fig. 1) in the restored reach in 1998.

For electrofishing, a direct current device DEKA 7000 (Mühlenbein, Marsberg, Germany) was used. The length of the fished river sections at the individual monitoring sites was measured in the middle of the river and ranged from 130 m to 180 m. These monitoring sites were chosen in a way that all habitat types were represented proportionally and enough area of each habitat was covered to limit stochastic variability in the fishing results. Fishing was carried out midstream and along both riverbanks, and each of these transects were fished twice, once drifting downstream without engine power, and a second time upstream with aid of the boat’s engine, resulting in a total of six passages of each site per year. At the broader restored river reaches, the midstream passage was divided into two: left midstream and right midstream, resulting in eight passages per site. All fish were recorded and counted per species.

Ecological traits of fish species

We used species trait information provided in the www.freshwaterecology.info database (Schmidt-Kloiber & Hering 2015). We selected traits that were related to four main trait groups that we considered relevant for a species response to restoration, habitat-related traits (general habitat preference, rheophily, feeding habitat, reproductive habitat), morphology and dispersal-related traits (migratory behavior, body length, shape factor, swim factor), feeding-related traits (feeding type) and reproduction-related traits (lifespan, age of female maturity, number of spawning runs, fecundity). We only included traits for which values for at least 90% of the species were available; the remaining gaps were filled from the sources Kottelat & Freyhof (2007) and fishbase.org (Froese & Pauly 2014). We furthermore checked for autocorrelation between traits. For cyprinid hybrids (mostly interbreeds of *Rutilus rutilus* and *Abramis brama*), we used average traits from these species and for *Carassius auratus*, traits of *Carassius gibelio* were used. Missing values for swimming factor (height of caudal peduncle/tail fin height) (Poff & Allan 1995; Scarnecchia 1988) and shape factor (body length/height) (Poff & Allan 1995) were determined by measuring the required lengths in photographs in Kottelat & Freyhof (2007).

Analysis of fish response to restoration

All statistical analyses were performed in R 3.1.1 (R Core Team 2014).

To account for differences in sampling effort (sites differed in length and number of passages, failure to sample all reaches in 1998, different number of replicate sampling sites in the restored and unrestored control reaches), a rarefaction approach was used (Gotelli & Colwell 2001), standardizing fish abundances for sampling section lengths of 150-m and two electrofishing passages. One out of 39 species was lost in this rarefaction, *Leuciscus idus*, which has originally been recorded once at a single site (L4) in 1997. To compare the similarity of species response to restoration we first calculated the net restoration effect for each species as the difference in species abundances between restored and control reaches for each year. We then used six parameters to characterize the resulting net restoration response curve of each species, based on which we clustered the species to explore common response patterns. These six parameters were (i) presence or absence of a changepoint, (ii) presence or absence of a short-term effect, (iii) delay between restoration and the onset of a restoration effect, (iv) Cohen´s D effect size of the restoration, (v) interannual variability of species abundances, and (vi) continuous linear trends in the species abundance.

The R package “changepoint” (Killick & Eckley 2014) was used to check whether a species responded to the restoration by a distinct increase (or a decrease) in abundance. The method was set to “AMOC” (at most one changepoint). To screen for short-term effects (ii), we repeated the changepoint analysis, this time using the “SegNeigh” method which allows for multiple changepoints. With the setting “Q=3” we allowed for two changepoints. Positive or negative temporary deflections in abundance were accepted as short-term effects only if they occurred in the first 5 years after the restoration was completed (i.e. between 1997 and 2002). Such a temporary increase or decrease in abundance was coded with 1 and -1, respectively, while absence of such a short-term effect was coded with 0. SegNeigh is an exact method, using cumulative sums test statistics, and is applicable to non-normally distributed data (Auger & Lawrence 1989; Scott & Knott 1974). (iii) The delay of the onset of a restoration effect was calculated as the number of years between restoration in the year 1997 and the changepoint. For species showing no changepoint, the delay was set to 0, as the following clustering procedure was incapable of handling NA values. (iv) Cohen´s D effect size for each species was calculated as the relative change of species abundance before and after the changepoint, standardized by the standard deviation (SD) as a measure of interannual variability of species abundance. No changepoint led to an effect size of 0. (v) To characterize the interannual variability in the time series on net restoration effect in each species, we calculated the standard deviation (SD) over all data per species if no changepoint was present;

if a changepoint was detected, we calculated the SD separately for the intervals before and after the changepoint and used a weighted average by the length of the interval as an estimation of SD. (vi) Continuous trends in the net restoration effect curves were assessed using a linear model, modeling each species against the timeline; if the p-value of the slope was significant (< 0.05) we noted the slope, the lack of a significant linear trend was coded with 0.

Before cluster analysis, data on all six parameters that characterized species responses to restoration were z-transformed. Autocorrelation between the six variables was checked. The cluster analysis based on Euclidean distances was performed in the R package “cluster” (Maechler et al. 2014) and significant clusters were determined using the package “clustsig” (Whitaker & Christman 2014).

Relating species response to restoration to species traits using Bioenv

To identify and select those species traits that best explained the similarity in the response of different species to this river restoration project, we used “Bioenv” analysis from the R package “vegan” (Oksanen et al. 2014). Bioenv selects the best subset of environmental variables by maximizing the correlation between environmental and community response distance matrices. Environmental variables were replaced by species traits in this application. To calculate distances in species traits, Gower distances were used to accommodate for categorical variables (Gower 1971). Correlation was performed based on Spearman’s rank sums. By this analysis, we determined which subset of species traits best explains the response of all species to restoration. To test for the significance of the best Bioenv models, we performed Mantel tests on the distance matrices of the selected species traits and fish species response to restoration using the dissimilarity based function of the R package “ecodist” (Goslee & Urban 2007).

To visualize the Bioenv results, we performed a principal coordinate analysis (PCoA), which compresses all variables into a two-dimensional plot, simultaneously reducing contortion utilizing the R package “FactoMineR” (Husson et al. 2014). We fitted the best variables from Bioenv.

Results

Community level

Total fish abundance and species richness was very similar at the restored and the control reaches before the restoration was carried out (Fig. 2). After the restoration, both total fish abundance and species richness increased at the restored reach, while it remained unaffected at the unrestored control reach. Total fish abundance showed a short-term overshooting response at the restored reach three years after the restoration was completed, followed by a return to more stable conditions at approx. three to four times the abundance of the unrestored control reach (Fig. 2A). However, a considerable level of interannual variability remained.

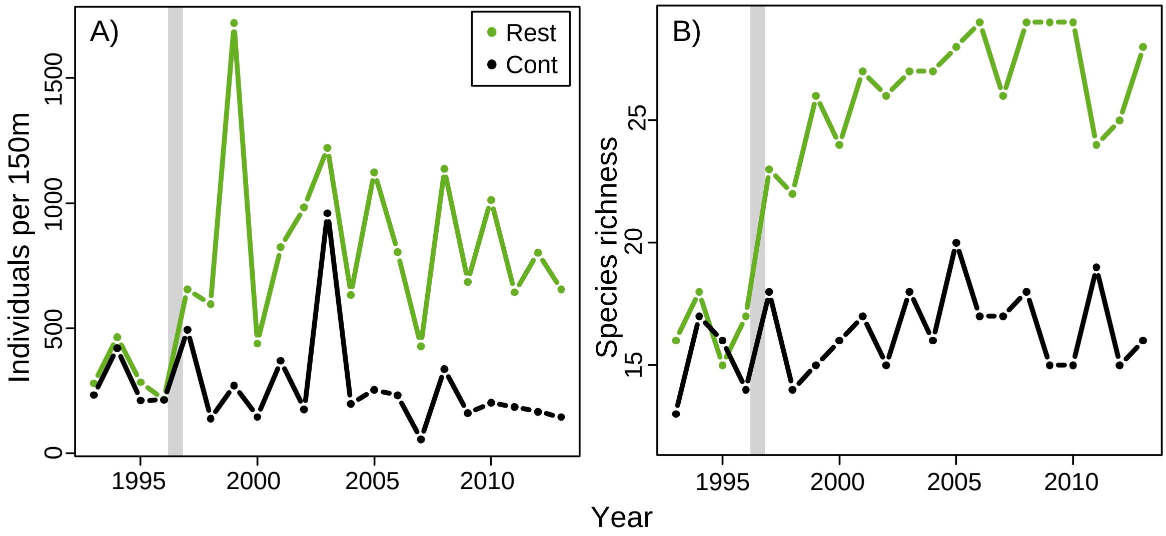

Figure 2: (A) Total fish abundance and (B) species richness in the Lippe River between 1993 and 2013 at the restored (Rest, green) and unrestored control reaches (Cont, black). The execution of the restoration project is marked by the gray vertical bar.

For species richness, no overshooting response was detectable and interannual variability was smaller than in fish abundance (Fig. 2B). After 5 to 7 years, species richness stabilized at almost the double value of the unrestored control reach. All species that belong to the set of reference species indicating good ecological conditions for this part of the Lippe River were present (Table 1) except *Salmo salar* and *Petromyzon marinus*, which were excluded from the upper and middle Lippe by a migration barrier until 2013; *Misgurnus fossilis*, which is missing in the entire Lippe catchment; and *Carassius carassius*, which is known from surrounding Lippe reaches, but is very rare.

Table 1: List of species detected by electrofishing at the restored and unrestored control reaches of the Lippe River between the years of 1993 and 2013. Values of the six response parameters of species response to restoration are reported. In species where no changepoint was evident, no delay could be calculated (NaN). *Leuciscus idus* was removed from the species list during the sample rarefaction routine (NA). Species that belong to the set of reference species indicative for good ecological conditions in this part of Lippe River are marked with * (NZO GmbH & IFÖ 2007). [1]Scientific name according to Kottelat & Freyhof (2007): *Cottus rhenanus*. [2]Scientific name according to Kottelat & Freyhof (2007): *Gasterosteus gymnurus*.

Species latin name	Species code	Changept (pres/abs)	Short effect (pres/abs)	Delay (years)	Effect size (Cohen's D)	Variability (SD)	Slope abline
*Abramis brama**	Abb	1	1	3	-0.92	4.66	0
*Alburnus alburnus**	Ala	1	1	4	-0.65	8.71	0
Alburnoides bipunctatus	Alb	0	0	NaN	0	0.11	0
*Anguilla anguilla**	Ana	0	0	NaN	0	11.72	0
Aspius aspius	Asa	0	0	NaN	0	0.44	0.03
*Barbatula barbatula**	Bab	1	0	16	2.26	30.91	0
*Barbus barbus**	Bar	1	0	8	0.84	13.02	0
*Blicca bjoerkna**	Blb	1	0	15	-0.76	2.12	0
Carassius auratus	Caa	0	0	NaN	0	0.15	0
Carassius gibelio	Cag	0	0	NaN	0	0.31	0
*Chondrostoma nasus**	Chn	1	0	3	0.91	31.81	0
*Cobitis taenia**	Cot	1	0	6	2.23	10.98	2.11
*Cottus gobio**,[1]	Cog	1	0	7	-1.25	27.64	0
Cyprinid bastards	Cyb	0	0	NaN	0	0.06	0
Cyprinus carpio	Cyc	1	0	5	1.05	0.86	0
*Esox lucius**	Esl	0	0	NaN	0	2.20	0

*Gasterosteus aculeatus**[2]	Gaa	1	0	16	5.11	8.38	1.22
*Gobio gobio**	Gog	1	0	12	1.69	92.25	10.72
*Gymnocephalus cernua**	Gyc	1	1	7	-0.59	2.82	0
*Lampetra planeri**	Lap	1	1	3	1.06	3.52	0
Lepomis gibbosus	Leg	0	0	NaN	0	0.40	0
*Leucaspius delineatus**	Led	1	0	14	2.30	8.33	0
*Leuciscus idus**	Lei	NA	NA	NA	NA	NA	NA
*Leuciscus leuciscus**	Lel	1	0	6	1.98	36.76	5.51
*Lota lota**	Lol	1	0	16	-6.12	5.09	-1.26
Oncorhynchus mykiss	Onm	0	0	NaN	0	0.05	0
*Perca fluviatilis**	Pef	1	0	10	0.64	11.37	0
*Phoxinus phoxinus**	Php	1	0	17	8.82	0.73	0
Poecilia reticulata	Por	0	0	NaN	0	0.05	0
Pseudorasbora parva	Psp	1	0	11	1.64	0.64	0.06
*Pungitius pungitius**	Pup	1	1	17	2.80	3.10	0
*Rhodeus amarus**	Rha	0	0	NaN	0	0.19	0.01
*Rutilus rutilus**	Rur	1	1	2	1.12	207.46	0
*Salmo trutta**	Sat	1	1	1	2.05	0.78	0
Sander lucioperca	Sal	0	0	NaN	0	0.37	0
*Scardinius erythropthalmus**	Sce	0	0	NaN	0	0.82	0
*Squalius cephalus**	Sqc	1	0	8	1.32	37.50	0
*Thymallus thymallus**	Tht	0	0	NaN	0	1.12	0
*Tinca tinca**	Tit	0	0	NaN	0	0.72	0

Clustering individual species responses

Individual species responses to the restoration varied strongly (Table 1). Seventeen species showed a gradual or step-wise increase in abundance in response to the restoration, six species decreased in abundance and 15 species showed no quantitative response. Positive short-term effects were detected in seven species (Table 1), while there were no negative short-term effects.

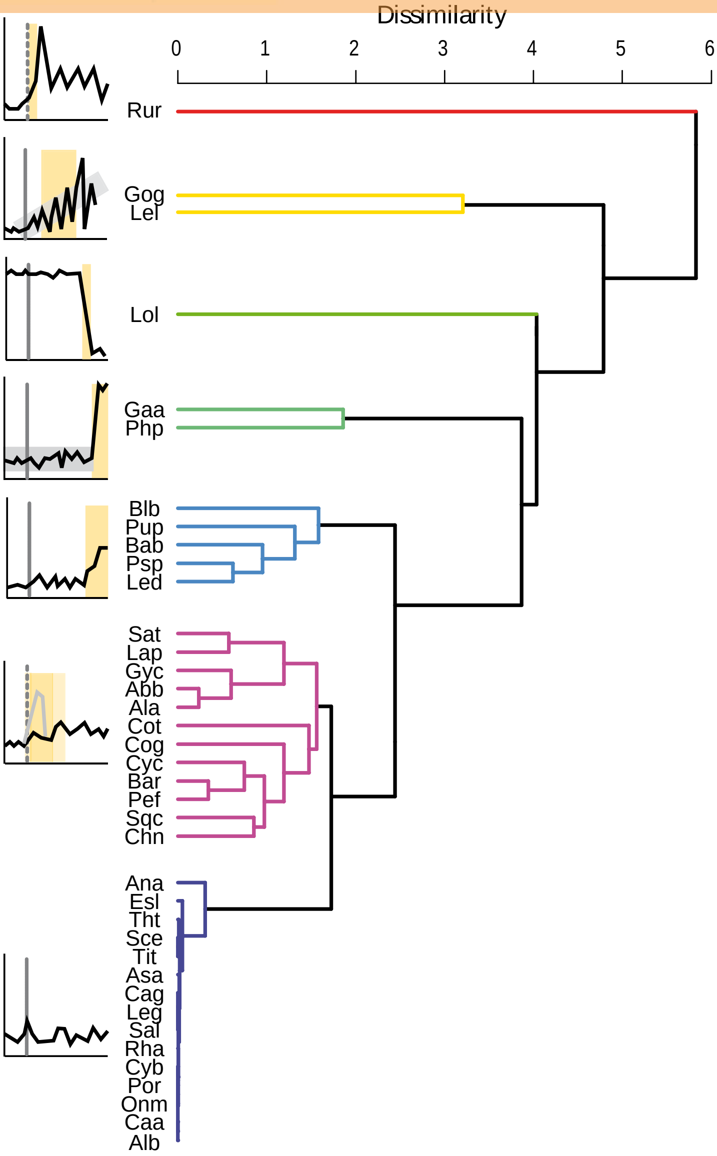

Figure 3: Cluster analysis on fish species' response to restoration based on the set of six species response parameters. The seven resulting groups were supported through significance tests. In response schematics, the orange color depicts when changepoints occurred and grey colors represent variability in species´ responses, and the dotted lines mark when the restoration was carried out. Full species names are given in Table 1.

Cluster analysis based on the six species response parameters to the restoration differentiated seven clusters (Fig. 3). Cluster 1 comprised only *R. rutilus*, which showed a strong overshooting response and high Cohen´s D value as well as considerable interannual variability in abundances (Fig. 3, Supplementary Table S1).

Species in cluster 2, *Leuciscus leuciscus* and *Gobio gobio*, also showed high interannual variability, but as an underlying pattern, a gradual increase in abundance. Cluster 3, comprising *Lota lota,* featured a strong negative Cohen´s D effect size. This unusual pattern, however, must be considered as an artefact caused by a strong increase of *L. lota* in the unrestored reach towards the end of the sampling period, which was paralleled by only a moderate increase in abundances in the restored reaches (Supplementary Figure F1). Cluster 4 with *Phoxinus phoxinus* and *Gasterosteus aculeatus* was defined by a strong positive effect size. The unifying characteristic of cluster 5 was a long delay until species responded. Cluster 6, in contrast, showed rapid responses with variable but overall positive Cohen´s D. From twelve species in cluster 6, five species showed a short-term effect, one showed a gradual increase and eight a positive Cohen´s D effect size. All non-responding species were grouped in cluster 7. Most of these species (twelve out of 15) furthermore were species that occurred in very low abundances (i.e. average densities across all sampling events of <1 individual per 50-m river length).

Relation between species responses to restoration and species traits

Out of the 13 species traits, lifespan, shape factor, spawning runs and female maturity were most strongly linked with individual species responses to restoration (Table 2). The addition of more species traits did not increase Spearman´s ρ further.

Table 2: Best set of species traits explaining the variability in fish species response to restoration based on Bioenv analyses. For each incremental model, a Mantel test on the significance of the correlation was performed.

Bioenv analysis		**Mantel test**	
Set of species traits	**Spearman´s ρ**	**Set of species traits**	**p-value**
Lifespan	0.11	Lifespan	< 0.01
+ Shape factor	0.12	+ Shape factor	0.16
+ Spawning runs	0.14	+ Spawning runs	0.14
+ Female maturity	0.15	+ Female maturity	0.08

With a maximum Spearman´s ρ of 0.15, the strength of the correlation in the Bioenv analyses was limited (Table 2). The best individual trait explaining species responses to restoration was life span. We used PCoA to illustrate the relationship between individual species responses to restoration and the relationship to species traits (Fig. 4). Only the first two axes had eigenvalues >1 and together these first two axes represented 65% of the total variability in the species response to restoration (Supplementary Table S2).

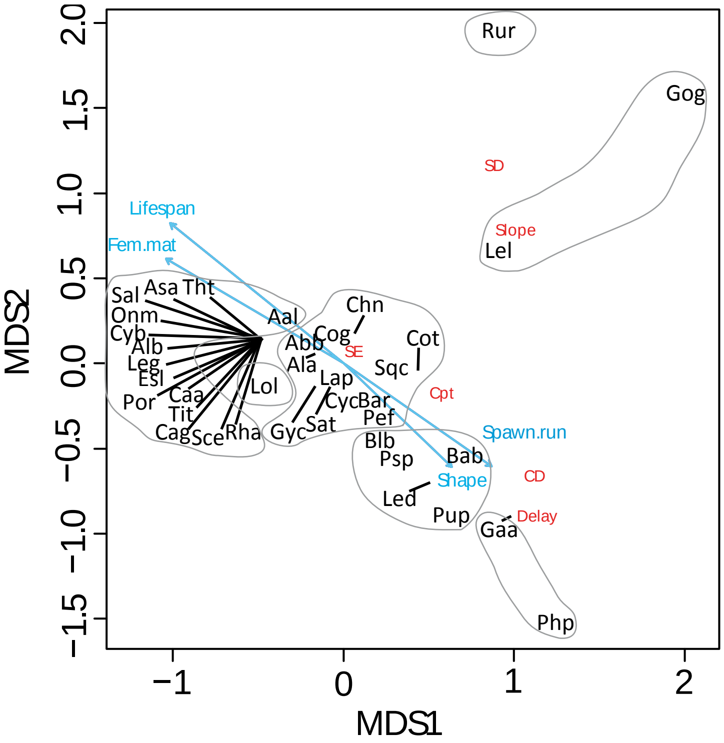

Figure 4: Principal coordinates analysis (PCoA) on the relationship between the response of the 38 fish species to the restoration and their species traits. The distance between individual species (in black; species abbreviation in Table 1) indicate the dissimilarity of their response to restoration with respect to the six response parameters (in red; Cpt = presence of changepoint, CD = Cohen's *D* effect size, Delay = response time of species, SD = interannual variability in abundance, SE = presence of short-term effect, Slope = gradual species response). The seven significant species response clusters are encircled. Blue arrows show the correlation of species traits to species responses to restoration. Only traits that were selected by the Bioenv model are presented: lifespan, age at female maturity (Fem. mat), shape factor (Shape), and number of spawning runs per year (Spawn.run).

Species that featured the highest Cohen´s D and delay values were those species with short life spans, early female maturity, several spawning intervals per year and a fusiform body shape (i.e. a high shape factor) (Fig. 4). Conversely, the cluster of non-responding species was characterized by long life spans, late female maturity, only one spawning interval per year, and deep-bodied shape. Species traits related less well to other parameters of species response to restoration, including the presence of changepoint, gradual changes in abundance, interannual variability in abundance and short-term effects.

Discussion

The restoration at Klostermersch in the Lippe River succeeded in diversifying and enhancing natural habitat structures (ABU 2010) and in increasing both species richness and abundances of fish over the ongoing monitoring period 17 years post-restoration. This positive biotic effect is coupled with various other ecosystem services, illustrating the multitude of socio-economic benefits of this restoration (ABU 2010). Consequently, this restoration project can be considered exemplary both in terms of outcomes and monitoring efforts, when compared to many other river restoration projects that have been carried out in recent years (Kail et al. 2015; Thomas et al. 2015).

Fish species exhibited highly varied and species-specific responses to restoration over the full 17-year monitoring period, making assessments based on unreplicated samplings appear questionable. Streams and rivers are highly dynamic and stochastic systems with high levels of interannual variability in communities, as was also the case in our study. This emphasizes the importance of more intensive monitoring efforts to reliably determine changes in community response to environmental changes in general (Haase et al. 2016) and restoration outcomes in particular (Vaudor et al. 2015). Basing the evaluation of restoration outcomes on a single sampling event, as is commonly done due to financial constraints, likely drives the high level of variability in perceived restoration outcomes. In this light, timing of sampling is critical for adequately determining restoration outcomes (Kail et al. 2015; Thomas et al. 2015). The likelihood of species present in the surroundings to establish at restored reaches is a function of time (Stoll et al. 2014; Tonkin et al. 2014). Schmutz et al. (2016) observed the greatest effect sizes in abundances within the first three years after completion of restoration (short-term overshooting response), and again in restorations older than 12 years. In the present study, strong successional processes lasted at least five to seven years before a stabilization of species richness and abundance was reached. Hence, earlier monitoring will not provide a “final” assessment of restoration effects. But even after this time, turnover in communities may occur. This development time to more stable communities is in line with other studies with river communities that also required approximately two to six years to develop (Langford et al. 2009). However, where nearby source populations were absent, recovery may take up to 50 years and more (Detenbeck et al. 1992; Langford et al. 2009), and is likely dependent on the recovery of the species pool. Indeed, recent work on German stream macroinvertebrate community responses to restoration showed that catchment-scale influences can override local restoration approaches, likely reflecting differences in overall species pools (Leps et al. 2016). These findings underscore the value of repeated monitoring over at least a decade to allow inclusion of secondary successional processes that take place at restored reaches, driving final restoration outcomes.

A re-convergence of communities to unrestored conditions, as observed in other recent studies (Kail et al. 2015; Thomas et al. 2015), was not observed. This likely reflects the fact that the present restoration, unlike many others, addressed relevant stressors at a sufficiently large scale. In turn, the ecological processes that support the provision of limited resources (e.g. dead wood, shallow open bays, clean gravel banks) were able to be reset, promoting sustained improvements in environmental conditions (Thomas et al. 2015).

All species that colonized the restored reach except one were known to be present in the regional species pool, and have been caught in various electrofishing campaigns conducted by the ABU at different occasions. This corroborates the findings of Stoll et al. (2014; 2013), who demonstrated that long-distance dispersal for the colonization of restored reaches is an exception. The only species not previously known from the species pool, the non-native, ornamental *Poecilia reticulata*, clearly has been released privately from a domestic aquarium. Previous electrofishing campaigns at the Lippe River have shown that the regional species pool from which this restoration could draw is diverse, with a total of 47 species known, including all except four species (*C. carassius*, *S. salar*, *P. marinus* and *M. fossilis*) that form the reference communities for this river type in the context of the EU WFD (Diekmann et al. 2005; NZO GmbH & IFÖ 2007). Hence, the common problem of regional species pools being impoverished and thereby limiting the colonization potential of restoration projects (Stoll et al. 2013) does not apply to the restoration project in the present study.

Individual species were affected differently by the restoration. There have been few attempts to describe the commonalities of species that respond favourably and unfavourably to habitat restoration. Examining the role of species traits in driving restoration responses, Stoll et al. (2014) and Mueller et al. (2014) found that rheophilic species disproportionally profited from river restoration (compared to limnophilic species), and abundances increased most strongly in invertivorous and omnivorous species (in contrast to piscivorous and other specialist feeding type species). Likewise, Schmutz et al. (2016) found that small, rheophilic species disproportionally profited from river restoration projects.

In the present study, body shape also differed between species with differing response characteristics to restoration. Slender-bodied, small species like *G. aculeatus*, *P. phoxinus* and *Leucaspius delineatus* showed the highest effect sizes. This result is generally attributed to the fact that most restorations aim to create riffles, shallow bankside habitats with low flow and activate floodplain water bodies. These are the habitat types that are commonly inhabited by small, slender-bodied species (Lorenz et al. 2013) but have typically become scarce in modified environments. The other three species traits that were identified in this study to affect species response to restoration were all related to life history and reproduction. Short-lived, fast-reproducing species profited from restoration, suggesting that species able to exert the strongest propagule pressure were best able to colonize newly available habitats. From community succession theory, and assuming a competition-colonization trade-off, it could be expected that such species with good colonization abilities are gradually displaced over time by species with slower reproduction, but higher competitive abilities (Li et al. 2015; Young et al. 2001). This displacement, however, was not observed in the 17 years of post-restoration monitoring at the Klostermersch restoration. Mueller et al. (2014) found species with comparatively long generation times and low abundances did not benefit a lot from restoration. Likewise, Ensign et al. (1997) report that species with fast recovery rates in the South Fork Roanoke River after a fish kill shared similar reproduction-related traits. This lack of long-term response of species with longer generation times and slower reproduction is unexpected. Future studies will have to determine whether succession processes in fish communities exceed the time frames commonly conceded in river restoration, or alternatively, if even at restored conditions, some critical stressors remained that prevented equal benefits in slow and fast reproducing species.

Habitat-related traits, like feeding habitat and spawning habitat, in contrast, were not correlated with species response to restoration. This indicated that the restoration measures were balanced across all habitat types and did not favour specialists bound to individual habitat conditions. A suite of non-native species was present at the restored reach (*Carassius auratus*, *Lepomis gibbosus*, *Oncorhynchus mykiss*, *P. reticulata*, *Pseudorasbora parva*), and in nearby reaches of the Lippe River. Müller et al. (2016) have shown that the trait composition of native and non-native fish species in Germany differ and thus invasion of non-native fish species leads to a long-term shift in the trait composition of communities.

In addition to species traits, occurrence rate and abundance of species in neighbouring reaches have been shown to determine colonization of restored reaches (Stoll et al. 2014; Stoll et al. 2013; Sundermann et al. 2011; Tonkin et al. 2014). This is in line with the hypothesis that predominantly species that can build up a critical propagule pressure will colonize restored reaches (Stoll et al. 2016). Therefore, rare and endangered species often do not profit from river restoration to a comparable extent (Huxel & Hastings 1999; Stoll et al. 2014; Thomas et al. 2015). Nevertheless, the positive examples of *L. lota*, *Cobitis taenia* and *Chondrostoma nasus* demonstrate that also rare and endangered species can profit from reach scale restoration projects.

Conclusions

Based on our findings, we conclude that analysis of species response patterns in relation to species traits can provide valuable insight into community processes at restored reaches and thereby further our conceptual understanding of river restoration (Bernhardt & Palmer 2011; Lake et al. 2007). Basing the analyses on species traits rather than taxonomic identities also allows for easier comparison and transfer of results across biogeographic borders into areas with different assemblages. Following on from our work, we believe a fruitful step would be for our approach to be implemented in comparative analyses on multiple restorations to corroborate our conclusions. Together with information on the community composition of the regional species pools, species traits can form a basis to develop predictive models on restoration outcomes that will help to enhance the effectiveness of restoration and allocate limited funds for restoration in the most promising way.

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Literature

ABU. 2010. Lippeaue - Eine Flusslandschaft im Wandel. Page 47. Bezirksregierung Arnsberg, Lippstadt, Germany.

ABU. 2013. Naturerlebnis Auenland. Arbeitsgemeinschaft Biologischer Umweltschutz im Kreis Soest e.V. (ABU), Soest.

Auger, I. E., and C. E. Lawrence. 1989. Algorithms for the optimal identification of segment neighborhoods. Bulletin of Mathematical Biology **51**:39-54.

Bernhardt, E. S., and M. A. Palmer. 2011. River restoration: the fuzzy logic of repairing reaches to repair catchment scale degradation. Ecological Applications **21**:1926-1931.

Detenbeck, N. A., P. W. DeVore, G. J. Niemi, and A. Lima. 1992. Recovery of temperate-stream fish communities from disturbance: a review of case studies and synthesis of theory. Environmental Management **16**:33-53.

Detering, U. 2008. Renaturierungsprojekte an der Lippe - Ergebnisse und Einschätzungen aus der Erfolgskontrolle. Schriftenreihe des Deutschen Rates für Landespflege **81**:71-75.

Diekmann, M., U. Dußling, and R. Berg 2005. Handbuch zum fischbasierten Bewertungssystem für Fließgewässer (FIBS). Fischereiforschungsstelle Baden-Württemberg, Langenargen.

EC. 2000. Directive 2000/60/EC of the European Parliament and of the Council establishing a framework for the Community action in the field of water policy (EU Water Framework Directive). Official Journal L 327.

Ensign, W. E., K. N. Leftwich, P. L. Angermeier, and C. A. Dolloff. 1997. Factors influencing stream fish recovery following a large-scale disturbance. Transactions of the American Fisheries Society **126**:895-907.

Froese, R., and D. Pauly. 2014. FishBase. World Wide Web electronic publication.

Goslee, S. C., and D. L. Urban. 2007. The ecodist package for dissimilarity-based analysis of ecological data. Journal of Statistical Software **22**:1-19.

Gotelli, N. J., and R. K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters **4**:379-391.

Gower, J. C. 1971. A general coefficient of similarity and some of its properties. Biometrics **27**:857-871.

Haase, P., M. Frenzel, S. Klotz, M. Musche, and S. Stoll. 2016. The long-term ecological research (LTER) network: Relevance, current status, future perspective and examples from marine, freshwater and terrestrial long-term observation. Ecological Indicators **65**:1-3.

Haase, P., D. Hering, S. C. Jähnig, A. W. Lorenz, and A. Sundermann. 2013. The impact of hydromorphological restoration on river ecological status: a comparison of fish, benthic invertebrates, and macrophytes. Hydrobiologia **704**:475-488.

Husson, F., J. Josse, S. Le, and J. Mazet. 2014. FactoMineR: Multivariate exploratory data analysis and data mining with R. R package version 1.27. URL: http://CRAN.R-project.org/package=FactoMineR.

Huxel, G. R., and A. Hastings. 1999. Habitat loss, fragmentation, and restoration. Restoration Ecology **7**:309-315.

NZO GmbH, and IFÖ. 2007. Erarbeitung von Instrumenten zur gewässerökologischen Beurteilung der Fischfauna, Chapter 9.6 (Steckbriefe Referenzen). - Report commissioned by Ministeriums für Umwelt und Naturschutz, Landwirtschaft und Verbraucherschutz des Landes NRW, under topical supervision by Regional District

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Government Arnsberg, Dez. 51.4 - Fisheries and Freshwater Ecology, Albaum, Germany. Page 61.

Kail, J., K. Brabec, M. Poppe, and K. Januschke. 2015. The effect of river restoration on fish, macroinvertebrates and aquatic macrophytes: a meta-analysis. Ecological Indicators **58**:311-321.

Killick, R., and I. A. Eckley. 2014. Changepoint: An R package for changepoint analysis. Journal of Statistical Software **58**:1-19.

Kottelat, M., and J. Freyhof 2007. Handbook of European freshwater fishes. Publications Kottelat, Cornol, Switzerland.

Lake, P. S., N. Bond, and P. Reich. 2007. Linking ecological theory with stream restoration. Freshwater Biology **52**:597-615.

Langford, T. E. L., P. J. Shaw, A. J. D. Ferguson, and S. R. Howard. 2009. Long-term recovery of macroinvertebrate biota in grossly polluted streams: Re-colonisation as a constraint to ecological quality. Ecological Indicators **9**:1064-1077.

Leps, M., A. Sundermann, J. D. Tonkin, A. W. Lorenz, and P. Haase. 2016. Time is no healer: Increasing restoration age does not lead to improved benthic invertebrate communities in restored river reaches. Science of the Total Environment **557-558**:722-732.

Li, F., A. Sundermann, S. Stoll, and P. Haase. 2015. A newly developed dispersal capacity metric indicates the succession of benthic invertebrates in restored rivers. PeerJ PrePrints **3**:e1835.

Lorenz, A. W., S. Stoll, A. Sundermann, and P. Haase. 2013. Do adult and YOY fish benefit from river restoration measures? . Ecological Engineering **61**:174-181.

Maechler, M., P. Rousseeuw, A. Struyf, M. Hubert, and K. Hornik. 2014. Cluster: cluster analysis basics and extensions.

Mueller, M., J. Pander, and J. Geist. 2014. The ecological value of stream restoration measures: An evaluation on ecosystem and target species scales. Ecological Engineering **62**:129-139.

Müller, F., M. Bergmann, R. Dannowski, J. W. Dippner, A. Gnauck, P. Haase, M. C. Jochimsen, P. Kasprzak, I. Kröncke, R. Kümmerlin, M. Küster, G. Lischeid, H. Meesenburg, C. Merz, G. Millat, J. Müller, J. Padisák, C. G. Schimming, H. Schubert, M. Schult, G. Selmeczy, T. Shatwell, S. Stoll, M. Schwabe, T. Soltwedel, D. Straile, and M. Theuerkauf. 2016. Assessing resilience in long-term ecological data sets. Ecological Indicators **65**:10-43.

Nilsson, C., L. E. Polvi, J. Gardeström, E. M. Hasselquist, L. Lind, and J. M. Sarneel. 2014. Riparian and in-stream restoration of boreal streams and rivers: success or failure? Ecohydrology:n/a-n/a.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner. 2014. Community Ecology Package "vegan".

Palmer, M. A., R. F. Ambrose, and N. L. Poff. 1997. Ecological theory and community restoration ecology. Restoration Ecology **5**:291-300.

Poff, N. L., and J. D. Allan. 1995. Functional organization of stream fish assemblages in relation to hydrological variability. Ecology **76**:606-627.

Radinger, J., and C. Wolter. 2014. Patterns and predictors of fish dispersal in rivers. Fish and Fisheries **15**:456–473.

Roni, P., K. Hanson, and T. Beechie. 2008. Global review of the physical and biological effectiveness of stream habitat rehabilitation techniques. North American Journal of Fisheries Management **28**:856-890.

Scarnecchia, D. L. 1988. The importance of streamlining in influencing fish community structure in channelized and unchannelized reaches of a prairie stream. Regulated Rivers: Research and Management **2**:155-166.

Schmidt-Kloiber, A., and D. Hering. 2015. www.freshwaterecology.info - an online tool that unifies, standardises and codifies more than 20,000 European freshwater organisms and their ecological preferences. Ecological Indicators **53**:271-282.

Schmutz, S., P. Jurajda, S. Kaufmann, A. W. Lorenz, S. Muhar, A. Paillex, M. Poppe, and C. Wolter. 2016. Response of fish assemblages to hydromorphological restoration in central and northern European rivers. Hydrobiologia **769**:67-78.

Scott, A. J., and M. Knott. 1974. A cluster analysis method for grouping means in the analysis of variance. Biometrics **30**:507-512.

Simaika, J. P., S. Stoll, A. W. Lorenz, G. Thomas, A. Sundermann, and P. Haase. 2015. Bundles of stream restoration measures and their effects on fish communities. Limnologica **55**:1-8.

Stoll, S., P. Breyer, J. D. Tonkin, D. Früh, and P. Haase. 2016. Scale-dependent effects of river habitat quality on benthic invertebrate communities - Implications for stream restoration practice. Science of the Total Environment **553**:495-503.

Stoll, S., J. Kail, A. W. Lorenz, A. Sundermann, and D. Haase. 2014. The importance of the regional species pool, ecological species traits and local habitat conditions for the colonization of restored river reaches by fish. PLoS ONE **9**:e84741.

Stoll, S., A. Sundermann, A. W. Lorenz, J. Kail, and P. Haase. 2013. Small and impoverished fish species pools are a main challenge to the colonization of restored river reaches. Freshwater Biology **58**:664-674.

Sundermann, A., S. Stoll, and P. Haase. 2011. River restoration success depends on the species pool of the immediate surroundings. Ecological Applications **21**:1962-1971.

R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Thomas, G., A. W. Lorenz, A. Sundermann, P. Haase, A. Peter, and S. Stoll. 2015. Fish community responses and the temporal dynamics of recovery following river habitat restorations in Europe. Freshwater Science **34**:975-990.

Tonkin, J. D., S. Stoll, A. Sundermann, and P. Haase. 2014. Dispersal distance and the pool of taxa, but not barriers, determine the colonization of restored river reaches by benthic invertebrates. Freshwater Biology **59**:1843–1855.

Vaudor, L., N. Lamouroux, J.-M. Olivier, and M. Forcellini. 2015. How sampling influences the statistical power to detect changes in abundance: an application to river restoration. Freshwater Biology **60**:1192-1207.

Whitaker, D., and M. Christman. 2014. Clustsig: significant cluster analysis. R package version 1.1. URL: http://CRAN.R-project.org/package=clustsig.

Whiteway, S. L., P. M. Biron, A. Zimmermann, O. Venter, and J. W. A. Grant. 2010. Do in-stream restoration structures enhance salmonid abundance? A meta-analysis. Canadian Journal of Fisheries and Aquatic Sciences **67**:831–841.

Young, T. P., J. M. Chase, and R. T. Huddleston. 2001. Community succession and assembly - comparing, contrasting and combining paradigms in the context of ecological restoration. Ecological Restoration **19**:5-18.

Supplementary materials

Table S1: Average values (± SD) of the six species response parameters to the restoration for each species clusters. Cluster variables which distinguish clusters are highlighted in bold. SD was only calculated for continuously scaled parameters and for clusters containing more than one species. Full species names are given in Table 1.

Cluster	**Changepoint (% species)**	**Short-term effect (% species)**	**Delay (years)**	**Effect size (Cohen's D)**	**Variability**	**Slope abline**	**Species**
1	100	100	2	1.12	**207.46**	0	Rur
2	100	0	9 ± 3	1.8 ± 0.1	64.5 ± 27.8	**8.1 ± 2.6**	Lel, Gog
3	100	0	**16**	**-6.12**	5.09	-1.26	Lol
4	100	0	**17 ± 1**	**7.0 ± 2.6**	4.6 ± 5.4	0.6 ± 0.9	Gaa, Php
5	100	20	**15 ± 2**	**1.7 ± 1.3**	9.0 ± 11.3	>0.0 ± >0.0	Bab, Blb, Led, Psp, Pup
6	1	**42**	**5 ± 3**	0.6 ± 1.1	12.8 ± 12.1	0.2 ± 0.6	Abb, Ala, Bar, Chn, Cog, Cot, Cyc, Gyc, Lap, Pef, Sat, Sqc
7	**0**	**0**	**0 ± 0**	**0 ± 0**	1.3 ± 2.9	**>0.0 ± 0.0**	Alb, Ana, Asa, Caa, Cag, Cyb, Esl, Leg, Onm, Por, Rha, Sal, Sce, Tht, Tit

Table S2: Results of principal coordinates analysis (PCoA) for four fish species trait variables (lifespan, shape factor, spawning runs, and female maturity), which led to best model in Bioenv analyses.

	MDS1	**MDS2**	**MDS3**	**MDS4**	**MDS5**	**MDS6**
Eigenvalue	1.73	1.12	0.72	0.62	0.17	0.05
Proportion explained	0.39	0.25	0.16	0.14	0.04	0.01
Cumulative proportion	0.39	0.65	0.81	0.95	0.99	1.00

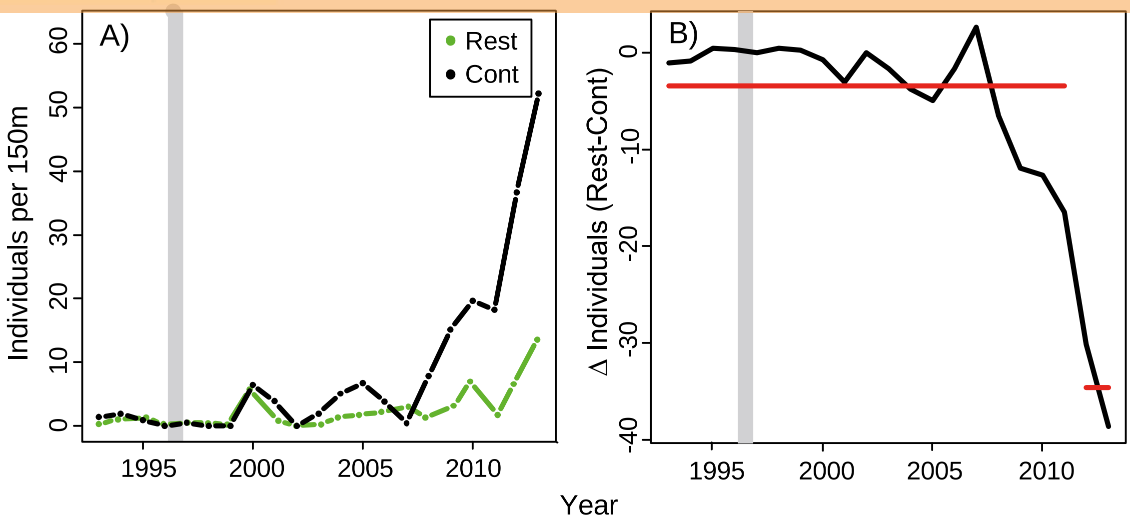

Figure S1: Response of *Lota lota* to the restoration at Klostermersch, Lippe River, Germany, between 1993 and 2013. The execution of the restoration project is marked by the gray vertical bar. (A) Rarefied abundances at the restored (Rest, green) and unrestored control reaches (Cont, black). (B) The analysis of species response patterns is based on the difference in abundance between the restored and control reach. Even though *L. lota* increased in abundance in the restored reaches, they did even more so in the unrestored control reaches, leading to a seeming decline, which was detected by the changepoint analysis (red line). The underlying reason is that reproduction and presence of young-of-the-year was concentrated in the restored reaches. Older individuals move to deeper river reaches where they settle in the interstices of rip-rap bank protection. This led to the misleading impression that *L. lota* declined in response to restoration.