Contributed Paper

Characterizing fish responses to a river restoration over 21 years based on species' traits

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Abstract: *Understanding restoration effectiveness is often impaired by a lack of high-quality, long-term monitoring data and, to date, few researchers have used species' trait information to gain insight into the processes that drive the reaction of fish communities to restoration. We examined fish-community responses with a highly resolved data set from 21 consecutive years of electrofishing (4 years prerestoration and 17 years postrestoration) at multiple restored and unrestored reaches from a river restoration project on the Lippe River, Germany. Fish abundance peaked in the third year after the restoration; abundance was 6 times higher than before the restoration. After 5–7 years, species richness and abundance stabilized at 2 and 3.5 times higher levels relative to the prerestoration level, respectively. However, interannual variability of species richness and abundance remained considerable, illustrating the challenge of reliably assessing restoration outcomes based on data from individual samplings, especially in the first years following restoration. Life-history and reproduction-related traits best explained differences in species' responses to restoration. Opportunistic short-lived species with early female maturity and multiple spawning runs per year exhibited the strongest increase in abundance, which reflected their ability to rapidly colonize new habitats. These often small-bodied and fusiform fishes typically live in dynamic and ephemeral instream and floodplain areas that river-habitat restorations often aim to create, and in this case their increases in abundance indicated successful restoration. Our results suggest that a greater consideration of species' traits may enhance the causal understanding of community processes and the coupling of restoration to functional ecology. Trait-based assessments of restoration outcomes would furthermore allow for easier transfer of knowledge across biogeographic borders than studies based on taxonomy.*

Keywords: bioenv analysis, long-term monitoring, overshooting response, regional species pool, stream restoration

Caracterización de las Respuestas de los Peces a la Restauración de un Río a lo Largo de 21 Años con base en los Atributos de las Especies

Resumen: *El entendimiento de la efectividad de la restauración está frecuentemente debilitado por la falta de datos de alta calidad de monitoreos de larga duración y, a la fecha, pocos investigadores han utilizado la información sobre las características de las especies para obtener conocimiento sobre los procesos que conducen la reacción de las comunidades de peces a la restauración. Examinamos las respuestas de las comunidades de peces con un conjunto de datos de alta resolución a partir de 21 años consecutivos de electropesca (4 años pre- y 17 años pos-restauración) en ramificaciones múltiples con y sin restauración de un proyecto de restauración en el río Lippe, Alemania. La abundancia de los peces alcanzó su máximo en el tercer año después de la restauración; la abundancia fue seis veces más alta que antes de la restauración. Después*

de 5–7 años, la riqueza y la abundancia de especies se estabilizó en niveles 2 y 3.5 veces más altos en relación a los niveles previos a la restauración, respectivamente. Sin embargo, la variabilidad interanual de la riqueza y abundancia de especies permaneció considerable, ilustrando el reto de valorar con confianza los resultados de restauración con base en los datos de muestreos individuales, especialmente en los primeros años después de la restauración. La historia de vida y las características relacionadas con la reproducción explicaron de mejor manera las diferencias en las respuestas de las especies a la restauración. Las especies oportunistas de vida corta con madurez temprana en las hembras y múltiples periodos de desove por año exhibieron el mayor incremento en la abundancia, lo que reflejó su habilidad para colonizar nuevos hábitats rápidamente. Estos peces fusiformes y generalmente de cuerpo pequeño viven comúnmente en áreas dinámicas y efímeras dentro de la corriente y de planicie inundable, objetivo frecuente de las acciones de restauración de hábitats de río, y en este caso su incremento en la abundancia indicó una restauración exitosa. Nuestros resultados sugieren que una mayor consideración de las características de las especies puede mejorar el entendimiento casual de los procesos comunitarios y el acoplamiento de la restauración con la ecología funcional. La utilización de las características para valorar los resultados de la restauración podría permitir una transferencia más sencilla de conocimiento a través de las fronteras biogeográficas que los estudios basados en la taxonomía.

Palabras Clave: análisis bioenv, monitoreo de larga duración, reservorio regional de especies, respuesta excedente, restauración de arroyos

Introduction

River restoration aims to return rivers to natural or near-natural conditions. So far, attempts to restore rivers have focused mainly on mitigating detrimental human influences on hydromorphological and physicochemical conditions, with the hope that communities will respond positively to these changes (Palmer et al. 1997). Comparative analyses show that these types of restoration have highly variable results from positive effects of restoration on resident biota (Whiteway et al. 2010; Kail et al. 2015; Thomas et al. 2015) to no clear effects (Sundermann et al. 2011; Haase et al. 2013; Schmutz et al. 2016).

This variability likely reflects several factors, for example, differences in the effectiveness of the restoration measures applied (Roni et al. 2008; Simaika et al. 2015); regional-scale environmental degradation that may override the effects of local habitat restoration (Bernhardt & Palmer 2011; Stoll et al. 2016); impoverished regional species pools resulting from historic degradation (Sundermann et al. 2011; Stoll et al. 2013, 2014); and restricted connectivity impeding colonization of restored reaches (Tonkin et al. 2014). Yet, even when one considers occurrence rates and abundances 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 processes that drive outcomes of restorations are not well understood. For this reason, Bernhardt and Palmer (2011) called for a shift in 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), a better conceptual understanding of processes at restored reaches can be gained. Ecological species' traits may inform restoration outcomes. Trait-based analyses provide a mechanistic linkage of the biotic response to environmental conditions, and observed effects show a greater temporal stability and are more consistent across broad spatial scales than taxonomic approaches (Culp et al. 2011). Relationships between fish-trait syndromes and environmental variation are well established (Winemiller & Rose 1992; Lamouroux et al. 2002; Frimpong & Angermeier 2010). In their seminal work, Winemiller and Rose (1992) differentiated 3 life-history strategies associated with distinct trait syndromes that are beneficial under different environmental conditions. Trait composition of communities changes with environmental degradation, especially with regard to flow regime (Meador & Goldstein 2005; Frimpong & Angermeier 2010; Mims & Olden 2013), and guild classifications based on traits is a common part of many biomonitoring schemes (Karr 1981; Hering et al. 2004). However, species' traits have not been commonly considered in studies on restoration outcomes, and where they have most studies focused on individual or limited sets of traits. For example, Li et al. (2015) showed that dispersal capacity of benthic invertebrates correlates with the colonization of restored sites, and Tullos et al. (2009) argue that taxa occurring in recently restored habitats are filtered for traits that are favored in disturbed environments. Rheophilic and invertivorous fish species profit disproportionally from restoration (Mueller et al. 2014; Stoll et al. 2014; Schmutz et al. 2016), and the reproductive success of lithophilic and psammophilic fish species increases the most (Lorenz et al. 2013).

To gain a more comprehensive understanding of the processes that form fish communities in restored rivers, we used a broad set of 13 species' traits that cover 4 distinct trait categories of potential importance in the context of colonization of a restored reach. These were traits related to habitat, feeding strategy, morphology and dispersal, and reproduction.

To quantify restoration effects, researchers commonly use pairwise comparisons (typically before–after or control–impact assessments) to assess species-specific

increases or decreases in richness or abundance in response to restoration. However, response trajectories of species may be complex and not necessarily synchronous because, for example, pioneering species may be displaced by more competitive species over time or species facilitation may lead to a step-wise increase in community complexity (Harper 1977). Therefore, multivariate classification of multiple time-step community-wide species' response curves should provide a more realistic description of species' reactions to restoration than analyses based on individual samplings. For this kind of analysis, addressing the functional understanding of community processes in restored rivers, repeated monitoring of entire communities prerestoration and postrestoration, and multivariate analyses of these data sets is necessary. Because monitoring is costly, however, such data sets are rare.

Due to this lack of real time series of data, there is still considerable uncertainty of the speed of recolonization processes at restored river reaches and the appropriate time to assess the final outcome of a restoration. Some restorations have been evaluated as early as half a year after completion of the restoration, whereas others have been monitored after only 19 years (Thomas et al. 2015). Research to detect temporal dynamics in restoration outcomes reveal contrasting results, including a positive correlation between the probability of species detection at restored reaches and time since restoration (Stoll et al. 2014; Tonkin et al. 2014); a long-term decrease in restoration effect (Kail et al. 2015); and a return of community composition to unrestored conditions (Thomas et al. 2015).

We analyzed patterns of species' responses to restoration in relation to species' traits, and we aggregated species' responses to evaluate the changes in the entire community over the monitoring period. We addressed the following questions: How do communities at restored reaches develop? When do these communities reach a state that allows a final evaluation of a restoration's outcome? Which distinct types of species' responses can be described based on a multimetric analysis of species' response curves? Which species' traits correlate with species' reactions to stream habitat restoration? And, which ecological strategies relate to the trait syndromes that are favored by restorations?

Methods

Restoration Project Study Site

We investigated a river-restoration project of the Lippe River, a tributary of the Rhine River in North Rhine-Westphalia, Germany. From 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, clearance of riparian vegetation, and increasing lateral erosion and incision through drainage of the floodplain for agriculture (ABU 2010, 2013). By 1990, the river banks were completely fixed and the Lippe River had lost approximately one-fifth of its original length (ABU 2010, 2013).

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 near Benninghausen. This first phrase covered an area and reach length of approximately 1.3 km² and 2 km, respectively (Fig. 1). To reestablish and connect the river's floodplain with the river bank, fixations were removed, the river was widened from about 18 to 45 m, the river bed was lifted by approximately 2 m, a series of small islands were built, full-grown trees were introduced as deadwood, drainage of the floodplain ceased and, finally, a number of flood channels and temporary standing water pools in the floodplain area were created (Fig. 1) (ABU 2010).

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, current velocity determines river-bed composition, and the river floods into the floodplain on at least an annual basis. None of these aspects were present in its channelized form (ABU 2010). Therefore, from a hydromorphological perspective, the restoration project is considered successful.

Survey of the Fish Communities

Electrofishing from a boat was carried out annually by Arbeitsgemeinschaft Biologischer Umweltschutz (ABU) personnel from 1993 to 2013 (4 years prior to restoration, 17 years after restoration) to monitor fish communities at the restored and unrestored reaches. Fishing was conducted at 4 sites (total length 635 m) within the restored river reach and at 2 unrestored control sites (total length 320 m) nearby, downstream of the restored reach (Fig. 1). The hydromorphological, hydraulic, and physicochemical structure of the control sites closely resembled unrestored conditions at the restored reach. Such detailed, long-term monitoring data from river-restoration projects are very rare. Sampling was carried out in August or September when discharge is stable and low and water transparency is high. Due to extreme floods, sampling was not possible at 2 of 4 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 to 180 m. These monitoring sites were chosen such that all structural features of the Lippe River
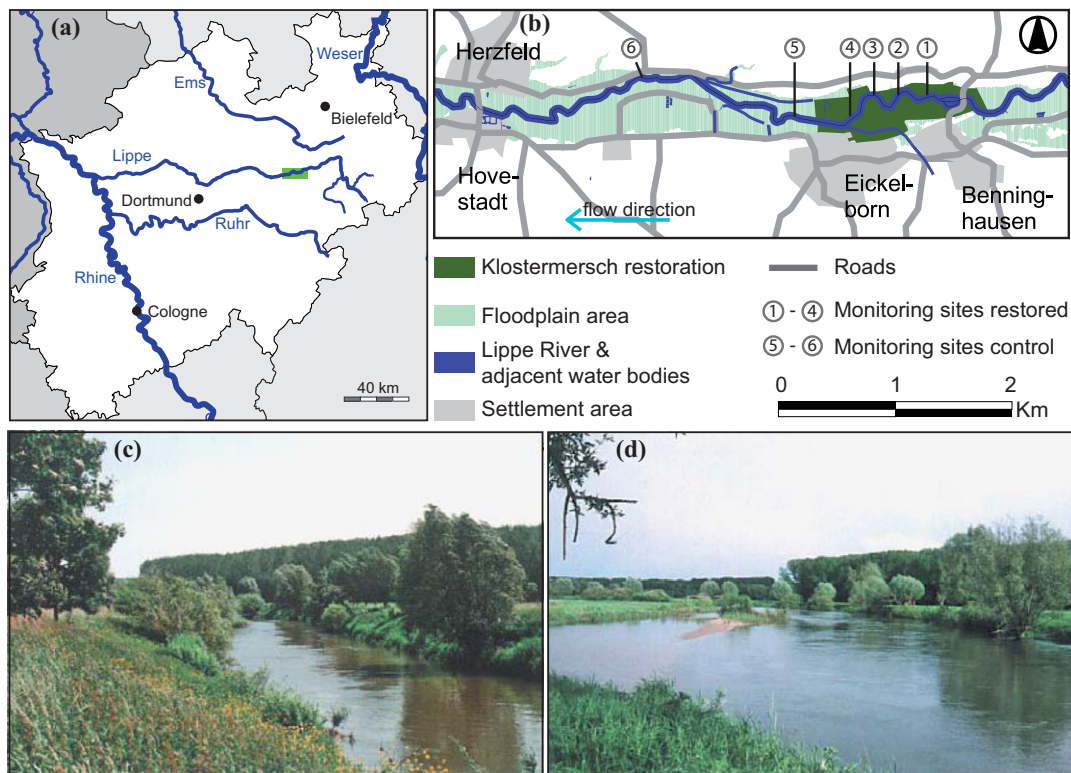
Figure 1. Overview of the river restoration project on the Lippe River, Germany: (a) location of the project (rectangle) in North Rhine-Westphalia, (b) Klostermersch (KM) restoration reach and the 6 sampling sites, (c) KM area before restoration (relatively straight river, carved deeply in its bed, no connection to riparian meadows), and (d) KM after restoration (river connected to meadows through a lift of the river bed, habitat spectrum widened through, for example, creation of sand banks and still-water areas). Photographs by J. Drüke.

(e.g., pools, riffles, sand bars, and dead wood) were represented proportionally and enough area of each type was covered to limit stochastic variability in the fishing results. Fishing was carried out midstream and along both riverbanks, and each of these transects was fished twice, once drifting downstream without engine power and a second time upstream with aid of the boat's engine, which resulted in 6 passages of each site per year. At the broader restored river reaches, the midstream passage was divided in 2 (left midstream and right midstream), which resulted in 8 passages per site. All fish were recorded and counted per species.

Ecological Traits of Fish Species

We used information on species' traits from the www.freshwaterecology.info database (Schmidt-Kloiber & Hering 2015). We selected traits from 4 main trait groups we considered relevant to a species' response to restoration. The first trait group was related to body morphology and dispersal (migratory behavior, body length, shape factor, and swim factor). Dispersal distance is a limiting factor in the colonization process of restored reaches for both macroinvertebrates (Sundermann et al. 2011;

Tonkin et al. 2014) and fish (Stoll et al. 2013, 2014), and dispersal ability directly relates to morphological traits (e.g., body size [Radinger & Wolter 2014]). The second trait group was related to foraging (feeding type), which is potentially relevant because food webs go through a successional process following establishment at restored reaches that entails complex intraspecific and interspecific dynamics in feeding guilds. The third group was related to species' habitats (general preference, rheophily, feeding habitat, and reproductive habitat) and was considered because restorations remodel habitat structures, creating new habitats and diminishing others. The fourth group of traits was related to reproduction and life-history characteristics (lifespan, age of female maturity, number of spawning runs, and fecundity), which are relevant to a species' ability to establish and maintain different levels of propagule pressure to facilitate colonization of new habitat (Winemiller & Rose 1992; Stoll et al. 2016). We considered only traits for which values for at least 90% of the species were available; the remaining gaps were filled from Kottelat and Freyhof (2007) and fishbase.org (Froese & Pauly 2014). We furthermore checked for autocorrelation among traits. For cyprinid hybrids (mostly of *Rutilus rutilus* and *Abramis brama*), we used

average traits, and for *Carassius auratus*, we used traits of *Carassius gibelio*. Missing values for the swimming (Scarnecchia 1988; Poff & Allan 1995) and shape factors (Poff & Allan 1995) were determined by measuring the required lengths in photographs in Kottelat and Freyhof (2007).

Fish Response to Restoration

All statistical analyses were performed in R version 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), we used a rarefaction approach in which we standardized fish abundances for sampling-section lengths of 150 m and 2 electrofishing passages. One out of 39 species was lost in this rarefaction, *Leuciscus idus*, which was originally recorded once at a single site (L4) in 1997.

To compare the similarity of species' responses to restoration, we first calculated the net restoration effect for each species as the difference in abundances of species between restored and control reaches for each year. We then clustered these net species' responses based on 6 response parameters we used to characterize the response curve of each species: presence or absence of a change point; presence or absence of a short-term effect; delay between restoration and onset of a restoration effect; Cohen´s *D* effect size of the restoration; interannual variability of species abundances; and continuous linear trends in species abundance.

We used the *R* package change point to check whether a species responded to the restoration with a distinct increase or a decrease in abundance and limited the number of accepted change points to 1 with AMOC (at most 1 change point) method.

To screen for short-term effects, we repeated the change-point analysis with the SegNeigh method, which allowed for 2 change points. 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 had been completed (i.e., 1997–2002). Such a temporary increase or decrease in abundance was coded with 1 and −1, respectively, whereas absence of such a short-term effect was coded with 0. SegNeigh is an exact method that applies cumulative sums test statistics and is applicable to non-normally distributed data (Auger & Lawrence 1989). The delay of onset of a restoration effect was calculated as the number of years between restoration in the year 1997 and the change point. For species showing no change point, the delay was set to 0 because the following clustering procedure could not handle not-available values. Cohen´s *D* effect size for each species was calculated as the relative change of species abundance before and after the change point

standardized by the SD as a measure of interannual variability of species abundance. No change point led to an effect size of 0. To characterize the interannual variability in the time series on net restoration effect in each species, we calculated the SD over all data per species if no change point was present. If a change point was detected, we calculated the SD separately for the intervals before and after the change point and used a weighted average by the length of the interval as an estimation of SD. Continuous trends in the net restoration-effect curves were assessed using a linear model that modeled each species against the timeline. If *P* of the slope was significant (<0.05), we noted the slope; lack of a significant linear trend was coded with 0.

Before cluster analysis, data on all 6 parameters that characterized species' responses to restoration were *z*-transformed. Autocorrelation between the 6 variables was checked. The cluster analysis based on Euclidean distances was performed in the *R* package cluster, and significant clusters were determined using the package clustsig, which is based on similarity of profile analysis (SIMPROF).

Relating Species' Responses to Restoration to Species' Traits with Bioenv

To identify and select species' traits that best explained the similarity in the response of different species to river restoration, we used Bioenv analysis in the R package vegan. Bioenv selects the best subset of environmental variables by maximizing the correlation between environmental and community-response distance matrices. We replaced environmental variables with species' traits in this application. To calculate distances in species' traits, we used Gower distances to accommodate for categorical variables. Correlation was performed based on Spearman's rank sums. With this analysis, we determined which subset of species' traits best explained 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' responses to restoration with the dissimilarity-based function in the R package ecodist.

To visualize the Bioenv results, we performed a principal coordinate analysis (PCoA), which compresses all variables into a 2-dimensional plot and simultaneously reduces contortion with the R package vegan. 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 (Fig. 2). Following the restoration, total fish
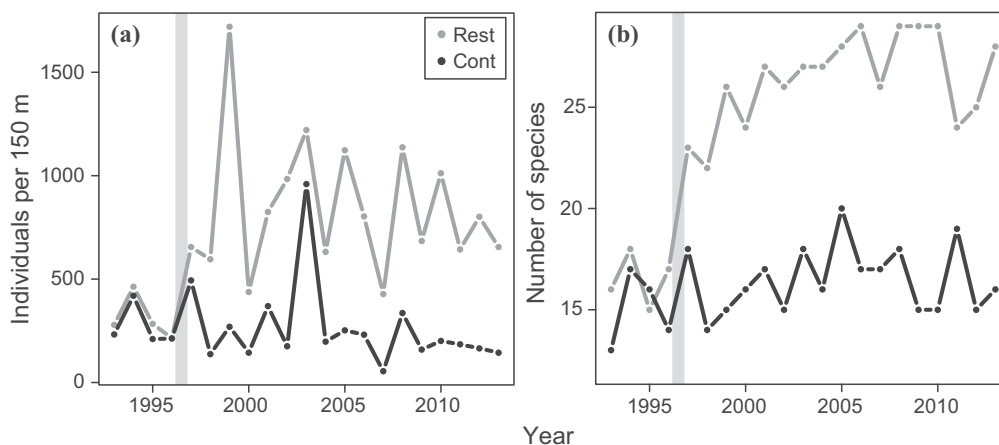
Figure 2. Total (a) fish abundance and (b) species richness in the Lippe River (Germany) from 1993 to 2013 in restored (Rest) and unrestored control reaches (Cont) (gray vertical bar, start of the restoration project).

abundance and species richness increased at the restored reach and remained unaffected at the unrestored control reach. Total fish abundance peaked in the third year after the restoration; abundances were 6 times higher than before the restoration. This increase was followed by a return to more stable conditions at approximately 3 times the abundance of the unrestored control reach (Fig. 2a). However, a considerable level of interannual variability remained. In individual years, percentage increase in abundance and species richness (control-impact comparisons) ranged from 27% in 2003 to 571% in 1999 and from 27% in 2011 to 94% in 2010, respectively (Fig. 2).

For species richness, no short-term peak was detectable and interannual variability was smaller than for fish abundance (Fig. 2b). After 5–7 years, species richness stabilized at almost twice that of the unrestored control reach. All species that belonged 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 absent in the entire Lippe catchment); and *Carassius carassius* (which is known from surrounding Lippe reaches but is very rare). All species that colonized the restored reaches except one (*Poecilia reticulata*) were present in regional species pool and had been caught in electrofishing campaigns conducted by the ABU on different occasions (Supporting Information).

Clustering Individual Species' Responses

Individual species' responses to restoration varied strongly (Table 1). Seventeen species showed a gradual or step-wise increase in abundance in response to the restoration, 6 species decreased in abundance, and 15 species showed no quantitative response. Positive short-term effects were detected in 7 species (Table 1); there were no negative short-term effects.

Cluster analysis based on the 6 response parameters differentiated 7 clusters (Fig. 3). Cluster 1 contained only *R. rutilus*, which showed a strong short-term increase in abundance, had a high Cohen's *D* value, and had considerable interannual variability in abundances (Fig. 3 & Supporting Information).

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 contained only *Lota lota,* which had a strong negative Cohen's *D* effect size. We considered this unusual pattern an artifact caused by aggregations of *L. lota* in the unrestored reach toward the end of the sampling period that was paralleled by only a moderate increase in abundances in the restored reaches. However, this species reproduced in restored reaches of the Lippe River (details in Supporting Information). 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' response. In contrast, species in cluster 6 responded rapidly and had variable but overall positive Cohen's *D* values. Of the 12 species in cluster 6, 5 showed a short-term effect, 1 a gradual increase, and 8 a positive Cohen's *D* effect size. All unresponsive species were grouped in cluster 7. Most of these species (12 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 segment).

Relationship 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

Table 1. Six response parameters of the species detected by electrofishing at the restored and unrestored control reaches of the Lippe River from 1993 to 2013.

Scientific name	Species code	Change point (presence or absence)	Short effect (presence or absence)	Delay (years)[a]	Effect size (Cohen's D)	Variability (SD)	Slope abline
Abramis brama [b]	Abb	1	1	3	−0.92	4.66	0
Alburnus alburnus [b]	Ala	1	1	4	−0.65	8.71	0
Alburnoides bipunctatus	Alb	0	0	NaN	0	0.11	0
Anguilla anguilla [b]	Ana	0	0	NaN	0	11.72	0
Aspius aspius	Asa	0	0	NaN	0	0.44	0.03
Barbatula barbatula [b]	Bab	1	0	16	2.26	30.91	0
Barbus barbus [b]	Bar	1	0	8	0.84	13.02	0
Blicca bjoerkna [b]	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 [b]	Chn	1	0	3	0.91	31.81	0
Cobitis taenia [b]	Cot	1	0	6	2.23	10.98	2.11
Cottus gobio [b,c]	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 [b]	Esl	0	0	NaN	0	2.20	0
Gasterosteus aculeatus [b,d]	Gaa	1	0	16	5.11	8.38	1.22
Gobio gobio [b]	Gog	1	0	12	1.69	92.25	10.72
Gymnocephalus cernua [b]	Gyc	1	1	7	−0.59	2.82	0
Lampetra planeri [b]	Lap	1	1	3	1.06	3.52	0
Lepomis gibbosus	Leg	0	0	NaN	0	0.40	0
Leucaspius delineatus [b]	Led	1	0	14	2.30	8.33	0
Leuciscus idus [b,e]	Lei	NA	NA	NA	NA	NA	NA
Leuciscus leuciscus [b]	Lel	1	0	6	1.98	36.76	5.51
Lota lota [b]	Lol	1	0	16	−6.12	5.09	−1.26
Oncorhynchus mykiss	Onm	0	0	NaN	0	0.05	0
Perca fluviatilis [b]	Pef	1	0	10	0.64	11.37	0
Phoxinus phoxinus [b]	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 [b]	Pup	1	1	17	2.80	3.10	0
Rhodeus amarus [b]	Rha	0	0	NaN	0	0.19	0.01
Rutilus rutilus [b]	Rur	1	1	2	1.12	207.46	0
Salmo trutta [b]	Sat	1	1	1	2.05	0.78	0
Sander lucioperca	Sal	0	0	NaN	0	0.37	0
Scardinius erythropthalmus [b]	Sce	0	0	NaN	0	0.82	0
Squalius cephalus [b]	Sqc	1	0	8	1.32	37.50	0
Thymallus thymallus [b]	Tht	0	0	NaN	0	1.12	0
Tinca tinca [b]	Tit	0	0	NaN	0	0.72	0

[a]*In species where no change point was evident, no delay could be calculated (NaN).*
[b]*Species that belong to the set of reference species indicative of good ecological conditions in this part of Lippe River (NZO GmbH & IFÖ 2007).*
[c]*Scientific name according to Kottelat and Freyhof (2007) Cottus rhenanus.*
[d]*Scientific name according to Kottelat and Freyhof (2007) Gasterosteus gymnurus.*
[e]*Leuciscus idus was removed from the species list during the sample rarefaction routine (NA).*

& Supporting Information). The addition of more species' traits did not increase Spearman's ρ further.

With a maximum Spearman's ρ of 0.15, the strength of the correlation in the Bioenv analyses was limited (Table 2), which is not uncommon with this type of ecological data.

Only the first 2 axes of the PCoA had eigenvalues >1, and together these first 2 axes represented 65% of the total variability in the species' response to restoration (Supporting Information). The PCoA illustrated the major gradient in species' responses from unresponsive species (Fig. 4, left), to species that exhibited short-term effects, and to species that exhibited population increases (Fig. 4, lower right). Higher Cohen's D effect sizes were associated with longer delays in species' response. Species with the highest Cohen's D values had short life spans, early female maturity, several spawning intervals per year, and a fusiform body shape (i.e., a high shape factor).
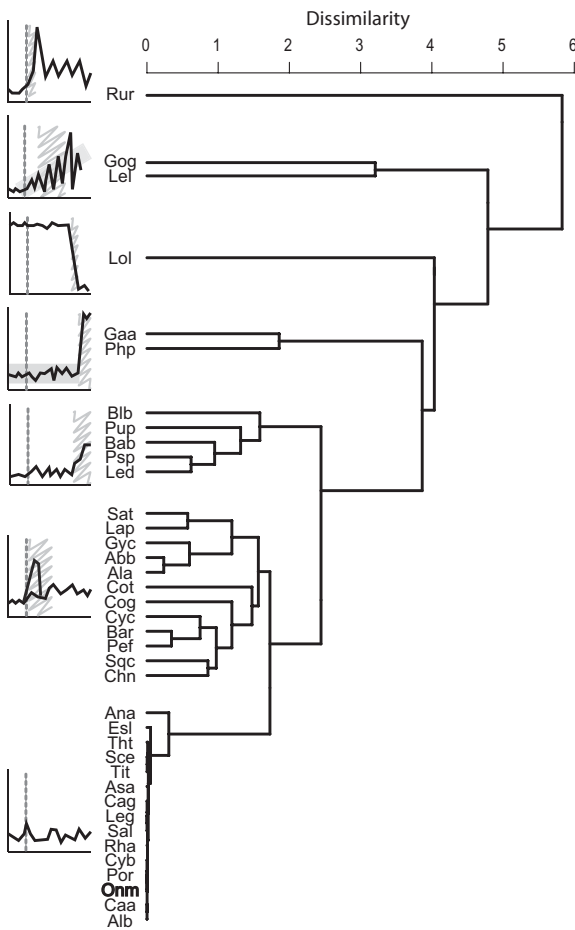
Figure 3. Results of cluster analysis of dissimilarity of fish species' response to restoration based on the set of 6 species-response parameters (see Methods) (gray zig-zag area, period in which a change point in species abundance occurred; gray shading, variability in species' responses; dashed lines, implementation of restoration; abbreviated names of species defined in Table 1). The 7 resulting groups were supported by significance tests.
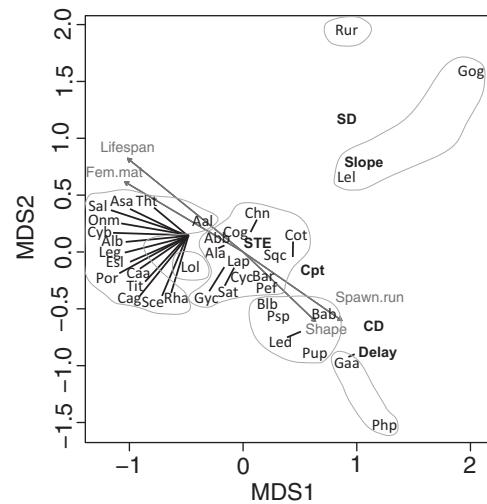

Figure 4. Results of principal coordinates analysis (PCoA) of the relationship between the response of the 38 fish species to river restoration and the species' traits selected by the Bioenv model (lifespan, age at female maturity [fem. mat], shape factor [shape], and number of spawning runs per year [spawn.run]). The distance between individual species (normal font) indicates the dissimilarity of their responses to restoration with respect to the 6 response parameters (bold font) (Cpt, presence of changepoint; CD, Cohen's D effect size; delay, response time of species; SD, standard deviation of interannual variability in abundance; STE, presence of short-term effect; slope, gradual species' response; gray arrows, correlation of species traits to species' responses to restoration; see Table 1 for definitions of abbreviations of species names and parameter values). The 7 significant species-response clusters are encircled.

Conversely, the cluster of unresponsive species was characterized by long life spans, late female maturity, 1 spawning interval per year, and deep-bodied shape. No specific traits could be identified related to response clusters 1 and 2 (Fig. 4, upper right), which were characterized by gradual increases in abundance and high interannual variability.

Discussion

The restoration at Klostermersch in the Lippe River succeeded in diversifying and enhancing natural habitat structures (ABU 2010) and correspondingly in increasing both species richness and abundances of fish over 17 years after restoration (monitoring is ongoing). Fish abundances exhibited a high interannual variability, and species' response curves to this restoration were complex and asynchronous, making assessment of restoration

Table 2. Best set of fish species' traits explaining the variability in species' responses to restoration based on Bioenv analyses in R.*

Bioenv analysis		Mantel test	
set of traits	Spearman's ρ	set of traits	P
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

For each incremental model, a Mantel test on the significance of the correlation was performed. The plus symbol refers to the incremental model structure. In each line, one variable is added to the model.

based on individual samplings questionable. This emphasizes the importance of long-term data sets to reliably determine restoration outcomes (Vaudor et al. 2015) and changes in fish community composition in response to environmental changes in general (Haase et al. 2016). Basing the evaluation of restoration outcomes on a single sampling event, as is commonly done due to financial constraints, adds to 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 nearby source populations facilitating reestablishment 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 3 years after completion of restoration (short-term peaks) and again in restorations older than 12 years. We found that strong successional processes lasted at least 5–7 years before some degree of stabilization of species richness and abundance was reached. This time to development of stable communities is in line with results of a number of other studies on river communities, including aquatic plants and invertebrate and fish communities that also required approximately 2–6 years to develop (Langford et al. 2009; Brederveld et al. 2011). There are examples, however, of gradual shifts in fish communities following restoration over at least 17 years (Shirey et al. 2016). Where nearby source populations were absent, recovery may take up to 50 years or more (Detenbeck et al. 1992; Langford et al. 2009). Recent work on stream macroinvertebrate community responses to restoration in Germany 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 and drive final restoration outcomes.

A reconvergence of communities to unrestored conditions that has been observed in other recent studies (Kail et al. 2015; Thomas et al. 2015) was not observed here. This likely reflects the fact that this 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, and clean gravel banks) were reset and thus promoted sustained improvements in environmental conditions (Bernhardt & Palmer 2011). Such recoveries of habitat are fundamental to the recovery of individual species.

Indeed, species were affected differently by the restoration. Similar to previous studies (Mueller et al. 2014; Stoll et al. 2014; Schmutz et al. 2016), we found that small, slender-bodied species such as *G. aculeatus*, *P. phoxinus*, and *Leucaspius elineates* showed the greatest effect sizes, although not all of them were rheophilic. This

outcome may have occurred because habitat restorations tend to focus on the creation of various shallow-water habitats, such as riffles, bays, sandbanks, and ephemeral floodplain water bodies that are rare in degraded rivers. These are the habitat types that are commonly inhabited by small, slender-bodied species (Lorenz et al. 2013).

The other 3 traits that affected species' responses to restoration were all related to life history and reproduction. These traits reflect the gradient between the opportunistic and periodic or equilibrium strategies as defined by Winemiller and Rose (1992). Opportunistic species characterized as short lived, early reproducing, and capable of spawning repeatedly throughout the year profited most from the restoration. Opportunistic species are well equipped to repopulate habitats over small spatial scales following disturbances (Lewontin 1965) because they can build up a high propagule pressure quickly, which has been identified as a key asset for the recolonization of restored river reaches for both fishes (Ensign et al. 1997; Stoll et al. 2013, 2014) and benthic invertebrates (Sundermann et al. 2011; Tonkin et al. 2014; Stoll et al. 2016). The re-creation of dynamic, ephemeral instream, and floodplain habitats was a focus of this restoration. Hence, opportunistic species not only dominated in the early years following restoration, reflecting the disturbance of the actual restoration work (Tullos et al. 2009), but profited long-term through the creation of intrinsically dynamic habitats.

Because colonization probability of restored reaches depends on propagule pressure in the surroundings, rare, and endangered species often do not profit from river restoration to the same extent as abundant species (Huxel & Hastings 1999; Stoll et al. 2014; Thomas et al. 2015). However, the positive examples of the rare and endangered *L. lota* (Supporting Information), *Cobitis taenia*, and *Chondrostoma nasus* in the Lippe River demonstrate that this is not always the case.

Species that did not respond to this restoration are relatively large, deep bodied, and long lived; exhibit late maturation; and typically spawn only once a year. These life-history traits entail slower reproduction and adhere to the periodic and equilibrium strategies in the conceptual framework of Winemiller and Rose (1992); these strategies are advantageous in relatively stable and uniform systems (equilibrium strategy) and large areas where habitat is patchy. The creation of such conditions was not a target of the Lippe River restoration.

Our methods allowed the identification of important traits linked with fish responses to restoration. Inclusion of additional traits that allow a better differentiation between periodic and equilibrium strategists, as well as traits reflecting the sensitivity of species to environmental fluctuations, may be useful in future studies to better resolve species' response types. Such analyses can provide valuable insight into community processes at restored reaches and thereby further conceptual

understanding of river restoration (Lake et al. 2007; Bernhardt & Palmer 2011). Identification of trait combinations linked to species' reactions to restoration seems therefore a promising way to compare and transfer results across biogeographic borders.

Acknowledgment

Supporting Information

(Appendix S1), All species that colonized the restored reach except one were known to be present in the regional species pool (Appendix S2), average values of the species' response parameters (Appendix S3), response of *Lota lota* to the restoration (Appendix S4), average values of species' traits within the clusters of species' responses to restoration (Appendix S5) and results of principal coordinates analysis, are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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