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Fish community responses and the temporal dynamics of recovery following river habitat restorations in Europe

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Abstract: Considerable uncertainty exists regarding the ability of reach-scale habitat restorations to promote ecological integrity and affect community composition in degraded streams and rivers and the time scales at which these effects take place. Restoration of habitats on the reach scale (hundreds of meters to a few kilometers) is expected to support threatened species because many of them are habitat specialists. In contrast, generalist species are predicted to be replaced in restored reaches. We used a large data set for 62 reach-scale restoration projects in 51 stream systems in Germany, Switzerland, and Liechtenstein and analyzed the changes in fish community composition induced by the restorations in terms of species richness, species turnover, Brillouin diversity index, total fish abundance, and proportion of alien and endangered species. We further analyzed the temporal dynamics of the fish community recovery over a period of 19 y postrestoration. Species richness and Brillouin diversity index increased in most of the restoration projects (66 and 57%, respectively), but recovery to historical reference conditions was not achieved. Total abundance was enhanced by most of the projects. Species composition in restored reaches underwent directed shifts for at least 10 y, with high and variable species turnover in the first years that decreased over time. The effects of restoration on Brillouin diversity index were highly variable in the first few years after restoration, but tended to increase over time. These dynamics must be considered more carefully in future protocols for evaluating restoration results, and final evaluation of restoration outcomes on fish communities should not be made too early. Our results indicate that reach-scale habitat restorations may be a suitable tool for increasing local fish abundance and slightly enhancing species diversity. However, more targeted approaches are needed to support threatened species and repress alien species.
Key words: meta-analysis, recolonization, stream, rehabilitation, success, failure, abundance, species diversity, species richness, endangered, invasive, evaluation

Over the last 3 decades, an increasing number of reach-scale river-restoration projects have been carried out to restore degraded rivers to more natural conditions (Bernhardt et al. 2005, Wohl et al. 2005). In the earlier phase of river restoration almost no monitoring of outcomes was done (Kondolf 1995, Bernhardt et al. 2005), but in recent years, an increasing number of case studies have been published (Alexander and Allan 2007, Comoglio et al. 2007, Nagle 2007, Baldigo et al. 2010, Buchanan et al. 2012). However, integration of these results is still rudimentary, and therefore, considerable uncertainty remains about the efficacy of river habitat restorations for achieving ecologically defined goals. In Germany (as throughout the European Union) and Switzerland, revised legislation requires restoration measures to increase the ecological quality of water bodies (Commission of the European Communities 2007, Schweizer Bundesamt für Umwelt 2009). This legislation will increase future investment in restoration projects. Therefore, information on the ecological benefits and limitations of restoration techniques for entire fish communities and for individual species is highly relevant and will help to improve future restoration programs.

Some studies affirm that defined hydromorphological goals (e.g., more heterogeneous flow pattern, natural river course and bed structures) commonly are achieved following restoration (Palmer et al. 2010, Jähnig et al. 2011, Stoll

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et al. 2013). More recently, indicators of ecological success have been developed to measure the benefits of restoration for biota (Woolsey et al. 2007). However, the metrics of ecological success used differed markedly among studies. This inconsistency makes it difficult to gain an overall picture of the benefits and limitations of river restorations in supporting natural species diversity. Nevertheless, the common tenor of many of these studies is that biological responses lag behind expectations (Roni et al. 2008, Palmer et al. 2010, Sundermann et al. 2011, Haase et al. 2013). The effectiveness of techniques is expected to vary along the stream continuum (Thomas 2014).

The timing of the evaluation may be particularly crucial for obtaining a reliable and comparable evaluation outcome. If the evaluation is made too early, slowly dispersing species may not have had the chance to colonize newly created habitats. On the other hand, if evaluation takes place too late, some newly created habitat features may have degraded again, especially when the scale of the restoration is much smaller than the scale of the actual environmental problem (Weigel et al. 2003). Lake et al. (2007) differentiated 4 general pathways of recovery following restoration and argued that recovery might be characterized by succession in species colonization rather than a straight line to a stable endpoint. Initial colonization relies on the dispersal abilities of stream fishes and is expected to vary considerably among species. Albanese et al. (2009) found that the speed of recolonization by fish species of abandoned stream sections was explained by the mobility of species. In the phase after initial colonization, basic ecological theory predicts that pioneer species will be replaced by species with good competitive abilities (Spieles 2010). Repeated sampling is preferable for analyzing the dynamics of restoration outcomes. However, only a few authors apply this time-consuming and expensive sampling scheme, so analysis of a large number of restoration projects, each sampled at a different point in time after the restoration work, may provide insight into the dynamics of species and community recovery in restored river reaches. Meta-analyses of large numbers of restoration projects also are useful for drawing general conclusions about the success of different restoration practices and guiding future restoration practice (Nagle 2007, Bernhardt and Palmer 2011).

Only a few attempts to summarize findings on the ecological outcomes of river-restoration projects have been published. Baldigo et al. (2010) analyzed the responses of fish communities to restorations that aimed to restore a natural channel design and found that overall community richness, diversity, and biomass increased as an effect of restoration at 4 of 6 sites, but that different species reacted differently. In contrast, Pretty et al. (2003) found no significant effects of addition of in-stream structures on fish species richness, abundance, or species composition in a study of 13 restoration projects. Roni (2003) also found limited effects on fish densities in a study of the response of benthic fish to the addition of large woody debris (LWD) in 29 North American rivers. Similar results were obtained by Kail et al. (2007), who assessed 50 river-restoration projects in Austria and Germany involving the addition of LWD. In the study by Kail et al. (2007), ecological outcomes lagged behind expectations, especially when compared with natural stream sections with an intact LWD regime. After analyzing a set of 18 restoration projects that used a wide range of restoration techniques, Stoll et al. (2013) found only marginal improvements in the fish communities. They attributed this lack of effect to limited dispersal capacities of fish and impoverished surrounding species pools from which restored river reaches could be colonized. A number of investigators focused on the effects of restorations on individual species or groups of fish, typically species that are interesting for anglers. For example, salmonids react positively in terms of abundance and biomass to the addition of artificial instream structures (Schlosser 1987, Stewart et al. 2009, Whiteway et al. 2010). The effects were visible mainly in smaller streams, where river health was good (Stewart et al. 2009). Lorenz et al. (2013) found that restorations have positive effects on population recruitment of already established species even though only few new species colonized restored reaches. Hence, the results of these meta-analyses are partly contradictory. As long as the focus of studies is on the response of limited sets of fish species (e.g., salmonids only) or on the effects of single restoration techniques (e.g., addition of LWD), generalization of the results will remain difficult.

First, we analyzed the reaction of entire fish communities based on species richness, abundance, and diversity to a wide range of restoration projects. From a conservationist's point of view, the proportion of endangered and alien species is of interest. Whether restorations are a suitable means to promote endangered fish species and to confine nonnative fish species is under debate (Kennard et al. 2005, Loo et al. 2009, Korsu et al. 2010). Second, we generated an overview of how the 46 most common fish species in Central Europe responded to restorations individually and summarized their response to restorations based on ecological species traits. Third, we assessed the temporal dynamics of the colonization process after the restoration work. To carry out those analyses, we gathered fish community data from 62 restoration projects and unrestored control reaches from Central Europe. Those projects represent typical stream habitat-restoration projects at the reach scale that aim to improve the general ecological quality of stream reaches. The projects were typical of central European restorations that have the goals of conserving and enhancing ecological diversity in general, instead of a single flagship species. Some restoration techniques are based on removal of artificial constructions (e.g.,

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for bank stabilization) to allow riverine self-organizing dynamics rather than on construction of static artificial habitats. Therefore, we excluded projects that focused on the reestablishment of connectivity because the resulting effects on fish species and communities are not related to changes in habitat quality but rather to facilitation of dispersal (Bond and Lake 2003, Doyle et al. 2005). The knowledge gained in such multirestoration data analyses provides insight into the potential of reach-scale river-restoration projects to support individual species and local fish communities. This insight enables more target-oriented planning of restoration projects and helps prevent costly failures in reaching restoration aims.

METHODS

Sampling sites

Projects used in our study contained both restorations and rehabilitations. Restoration is defined as the re-establishment of structure, functioning, diversity, and dynamics to historic reference conditions, whereas rehabilitation seeks to repair ecological processes and to increase ecosystem productivity as rapidly as possible (Aronson et al. 1993). The 2 terms have slightly different meanings, but we use restoration in our study because it is more commonly used for any efforts to bring rivers back to a more natural state.

We analyzed 62 reach-scale river-restoration projects in 51 streams and rivers in Germany, Switzerland, and Liechtenstein. Sites were distributed over an altitudinal gradient ranging from slow-flowing rivers in the German lowlands (minimum altitude = 7 m asl) to streams in the pre-alpine regions of Switzerland (maximum altitude = 572 m asl). The median was 285 m asl. The 39 German projects were in the central federal states of Bavaria, Hesse, North Rhine-Westphalia, Saxony-Anhalt, Lower Saxony, Schleswig-Holstein, and Rhineland-Palatinate. In Switzerland, most of the 21 projects were situated north of the alpine mountain range, but one project was on the southern side of the Alps in the Po drainage. Two projects were in Liechtenstein. Most of the projects (80%) were carried out in lower-order rivers with stream widths <15 m, but the data set also included some projects from larger rivers with widths up to 117 m (median = 7.0 m). All projects were attempts to enhance the naturalness of rivers and streams by creating diverse habitats to facilitate a more natural and diverse freshwater fauna. Some projects also were attempts to recreate longitudinal and lateral connectivity. These goals were addressed with a variety of individual techniques (Fig. 1), and in most projects, several methods (3.6 ± 1.8 [SD]) were used.

The length of the restored sections ranged between 100 and 12,000 m (median = 700 m). In the long restored reaches in particular, individual restoration techniques might have been realized only in sections rather than the entire stretch. Therefore, the restored net length might be shorter than indicated. The projects were undertaken between 1990 and 2009, but most were done after 1999. Outcomes were evaluated 1 to 19 y after construction. Half of all projects were evaluated <4 y post construction. In 9 projects, the effect of restorations on fish communities was assessed with a before–after restoration comparison approach. In the remaining 53 projects, an impact–control approach was applied based on fish data from the restored and nearby unrestored reaches from the same river. In all 62 projects, changes in the fish community were evaluated with species presence–absence data. Additional data on fish abundance were available for 57 projects. Fish abundance data were comparable between the restored and unrestored control reach within projects, but not among projects because sampling effort and procedure differed among projects. For example, some stretches were sampled with 1 electrofishing run, whereas others had up to 3 repeated runs per stretch.

Sampling protocols differed between Germany and Switzerland/Liechtenstein. Fish communities in Germany were sampled based on a standardized protocol compliant with the European Water Framework Directive (Diekmann et al. 2005). Sampling took place in August and September 2007 and 2008. The sampling was described in detail by Stoll et al. (2013). Fish data from Switzerland and Liechtenstein were provided by the cantonal administrations (environmental, fisheries, and hydroengineering departments) upon email request. Our request stated explicitly that all reports would be of interest, regardless of whether the project was considered successful or not. In return, the anonymity of project data was guaranteed to the cantons. Some additional data sets were extracted from scientific works, such as diploma theses and reports. Therefore, sampling protocols (sampling stretch, number of repeated electrofishing runs and season, when sampling took place) sometimes varied among projects. We used only relative numbers (percentages, ratios) resulting from a direct comparison between pairs of control and restored sites in our analyses. Therefore, differences in the efficiency of samplings between projects can largely be neglected. Seasonal differences in sampling dates might affect data from systems inhabited by migratory species. The number of migratory species in the Swiss rivers was very low, so we consider the effect of those inconsistencies as justifiable and small enough to permit us to analyze all projects together.

Data analysis

We organized data with a common data sheet that summarized relevant data on: 1) stream characteristics, 2) restoration method, 3) sampling protocol, and 4) species presence, or if available, abundance data at the restored

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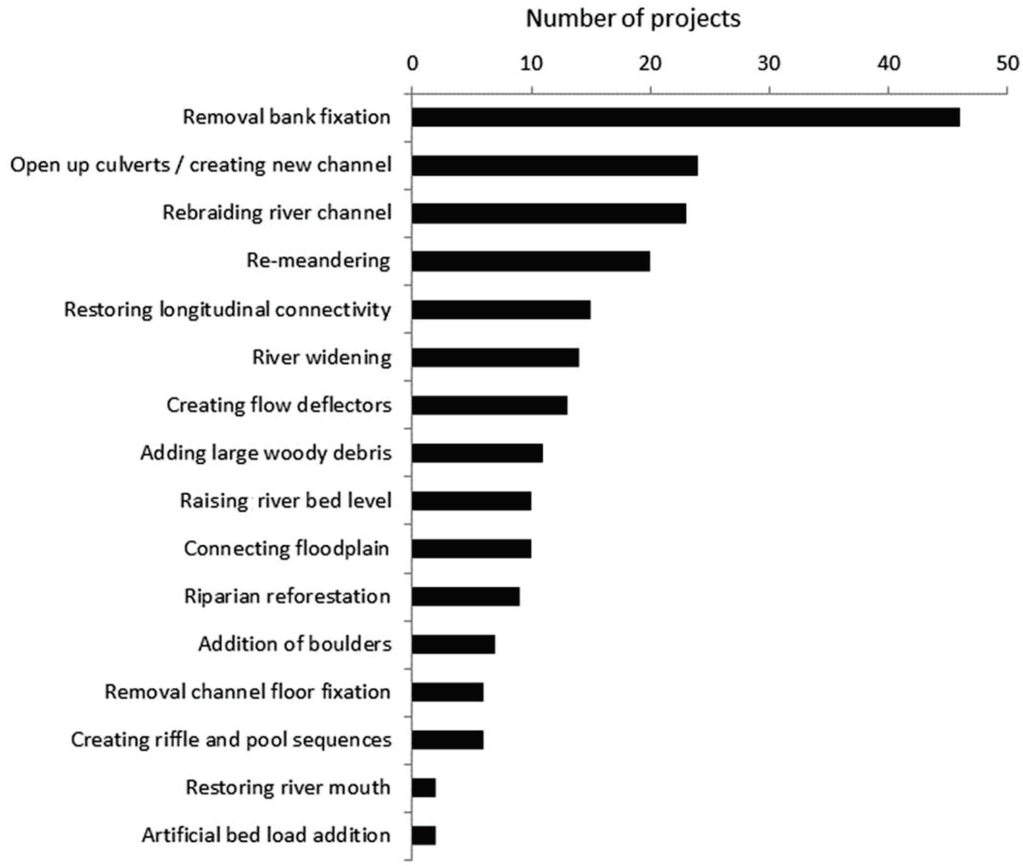

Figure 1. Overview of the frequency of restoration techniques realized (multiple techniques per project).

and control reaches. We assessed the length of the restored section, river width at the restored section, catchment area upstream of the restored section, and altitude as stream characteristics. We differentiated 16 individual restoration methods. On average, 3.6 of these methods were applied in each restoration (range: 1–9; Fig. 1). In the section on sampling protocols, we recorded whether restored reaches were sampled in a before–after restoration design or a restored and unrestored control reach were sampled simultaneously. We also recorded the time between implementation of the restoration and the sampling. Species abundance data from the restored and control reaches were standardized to a sampling area of 1 ha.

We used information on the threat status of each species from the Red List of Freshwater Fish Species of Germany and Switzerland (Bless et al. 1998, Kirchhofer et al. 2007), which are local adaptations of the International Union for Conservation of Nature (IUCN) red list, to calculate the change in abundance of endangered species. Data were applied for each country separately (Liechtenstein according to the Swiss red list). We grouped the 3 highest threat classes (nearly extinct, highly endangered, endangered) as endangered, and we did not consider extinct species. We assigned species that were potentially endangered to the group of not endangered fish. In Germany and Switzerland, 27 and 11 species, respectively, were defined as endangered. We calculated the proportion of endangered species in total fish abundance for restored and control sections.

We defined the following fish species as alien to German and Swiss streams: *Pseudorasbora parva*, *Micropterus salmoides*, *Leuciscus idus* (ornamental form), *Oncorhynchus mykiss*, and all species belonging to the genus *Lepomis* (mostly *Lepomis gibbosus*). *Sander lucioperca* was also considered as alien in the study streams because none of the catchments lay within the natural distribution range of this species (Kottelat and Freyhof 2007). Other species may have been alien to individual subcatchments where they did not occur naturally. However, such small-scale range expansions did not qualify for classification as an alien species because reliable historic references of occurrence were not available for all 46 species in the 51 streams.

We computed a suite of 6 metrics to evaluate the success of the restoration projects. These metrics evaluate the composition of local fish communities. Such metrics are commonly used in the analysis of river-restoration assessments (Weber and Peter 2011). These compositional metrics were: species richness at the restored reach, species

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turnover as a result of restoration, change in total fish abundance, change in species diversity, and changes in the proportions of endangered and alien species. We standardized abundance data to 1 ha of area sampled to calculate the difference in total fish abundance between restored and unrestored conditions. Species richness was the total number of species found, regardless of abundance. We calculated change in species richness as the difference in species numbers between restored and unrestored control reaches. We calculated species turnover as the sum of all species that either disappeared or newly appeared at a restored reach compared to the unrestored control. We used the Brillouin Index to calculate fish diversity based on abundance data standardized to sampling area. This index is suitable for electrofishing data because it is not sensitive to differences in sampling efficiency among methods (Pelz and Luebbers 1998). We were able to examine shifts in species diversity only in the 50 projects that provided abundance data and had >1 species present in both restored and unrestored control reaches.

We compared the number of projects for which these 6 metrics increased or decreased as a result of the restorations. To compensate for random fluctuations in total fish abundance and diversity, we defined a threshold value of 10% change, which is a typical threshold for identifying effects, e.g., in ecotoxicology (Shieh et al. 2001). We classified metrics for which changes were <10% as unchanged. We classified metrics for which changes were >10% as increased or decreased. For alien and endangered species richness, we used the same threshold (10%) to identify differences in species composition.

We carried out statistical analyses using R software (version 3.1.2; R Project for Statistical Computing, Vienna, Austria). We used general linear models to identify the characteristics of the restoration project that affected restoration success or failure for fish communities. Response metrics for fish communities included change in total fish abundance, change in species number, species turnover, and change in the Brillouin Index. We used altitude, restored reach length, time since restoration, river width, and catchment size as independent variables. Models were stepwise backward selected until the minimum Akaike Information Criterion (AIC) was reached. Significant relationships detected by the general linear models were further analyzed with quantile regression with the focus on temporal dynamics in restoration outcomes (Cade and Noon 2003). Quantile regressions are useful for wedge-shaped data distributions with unequal variation (Kail et al. 2012).

We used a Mantel test to assess whether increases or decreases in the abundances of individual fish species were related to individual restoration methods (Oksanen et al. 2013). Absolute values of changes in abundance (increases and decreases) were $\ln(x + 1)$-transformed. We used the function *vegdist* to calculate Euclidean distance matrices for restoration methods and changes in fish communities. Significance was assessed using 999 permutations. In a 2nd approach, we used redundancy analysis (RDA) to examine whether observed changes in fish community composition were related to the restoration methods applied. Significance was assessed using 999 permutations.

We used the net colonization rate to characterize the reaction of individual species to restorations. First, we compared the percentage of newly colonized reaches across all restoration projects to the number of reaches in which a species was already present at unrestored reaches. Second, we grouped species by their functional traits, as defined by Grenouillet and Schmidt-Kloiber (2006) for European freshwater species. We chose only traits that are logically linked to habitat alterations resulting from restoration: habitat preference, velocity preference, feeding habitat, and reproductive habitat. We assessed functional trait response on the basis of absence/presence and abundance. We summed the number of species per project with the defined trait over all projects and calculated the proportion that responded for each functional group of fishes. We compared the results for each functional group to the mean response of all species in all projects to visualize response trends by functional characteristics of species.

RESULTS

Community response

No significant relationship was detected between the restoration methods used in the individual projects and changes in abundances of individual fish species (Mantel test: $R = -0.12$, $p = 0.95$; permutation test following RDA: df = 15, $F_{305} = 1.17$, $p = 0.12$; Fig. S1). Total fish abundance increased in 58% of all projects (Fig. 2A). In 29% of the projects, fish abundance decreased in restored reaches relative to unrestored control reaches. Restoration-related changes in abundance were greater in high- than in low-elevation rivers (Table 1).

Species richness was greater in restored (9.4 ± 5.5 [SD]) than in unrestored control reaches (7.9 ± 5.7) (paired t-test: $t_{61} = 4.3$, $p < 0.001$). Species richness increased after restoration in 66.1% of all projects (Fig. 2B). In 9 projects (12.9%), fewer species were detected in restored than in unrestored control reaches. In 19.4% of projects, species richness did not differ between restored and unrestored control reaches. The increase in species richness at a restored reach was positively related to the width of the restored reach and upstream catchment area, and species richness at restored reaches was greater in lowland than in upland rivers (Table 1).

Species turnover in restored reaches was >30% of all species present in unrestored control conditions in 71% of the restoration projects. In most projects, the restored reach

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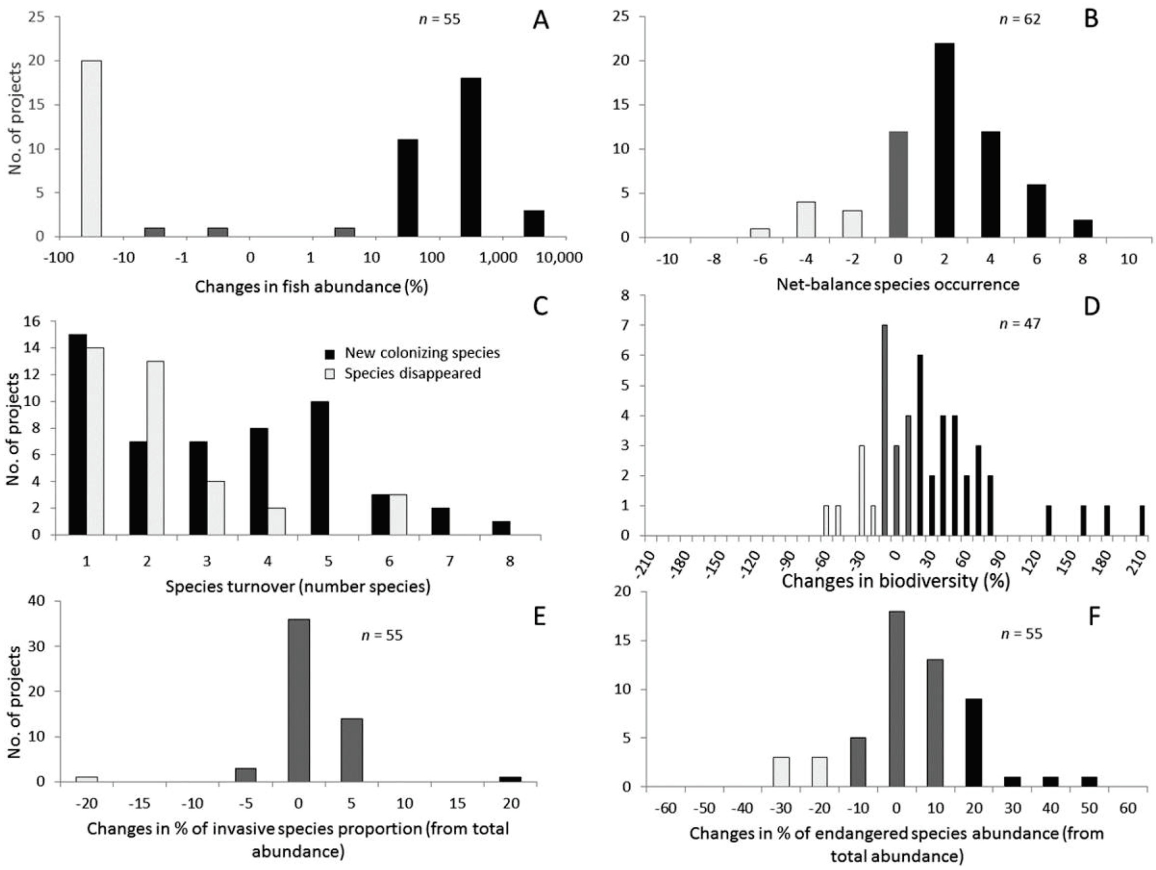

Figure 2. Percent change in total fish abundance (A), species richness (B), species composition (species turnover) (C), species diver sity (Brillouin Index) (D), proportion of alien species (E), and proportion of endangered species (F) in response to habitat restoration. See text for details of calculation of metrics. Black bars indicate a trait shift in the desired direction, gray bars indicate unchanged con ditions, and light gray bars indicate an undesirable response to restoration.

lost 1 or 2 species and gained 1 to 5 new species (Fig. 2C). Species turnover and the age of the restoration in years were inversely related (Table 1). Results of quantile regression (based on medians) and least-square regression (based on means) relating species turnover (ST) to the age of the restoration (t) were similar (quantile regression: $ST = 5.27 - 0.27t$; least-square regression: $ST = 5.20 - 0.26t$, $n = 62$, $R^2 = 0.12$, $p = 0.006$; Fig. 3A). Quantile regression further revealed that the variability in species turnover was particularly high in the first years after restoration (Fig. 3C). Slopes were stable and similar to the least-square regression slope over large central parts of the quantile range (Fig. 3A, E). In ~5% of projects, no species turnover occurred. Species turnover increased with the width of the restored reach (Table 1).

Species diversity, expressed by the Brillouin Index, showed a similar pattern to species richness. A large fraction of projects showed an increase in diversity (57%), whereas 28% showed reduced diversity. In 15% of projects, no change in diversity was observed (Fig. 2D). Overall, fish species diversity was greater in restored than in unrestored control reaches (paired t-test: df = 49, $t = 2.6$, $p = 0.013$). The change in fish species diversity (ΔDiv), expressed as the difference in Brillouin index between unrestored and restored control reaches, increased with the age of the restoration (Table 1). Results of the 2 regression approaches relating ΔDiv to the age of the restoration were very similar (quantile regression: $\Delta\text{Div} = -0.05 + 0.05t$; least-squares regression: $C = -0.02 + 0.05t$, $n = 50$, $R^2 = 0.08$, $p = 0.049$; Fig. 3B). Quantile regression showed that the change in species diversity was particularly variable in the first years after the restoration (Fig. 3D), when positive and negative effects on species diversity were recorded equally often. However, positive effects dominated with increasing age of the restoration (Fig. 3B, F). ΔDiv increased with catchment size (Table 1).

The 2 measures for functional subgroups (changes in the proportion of endangered and alien species) showed no overall trend with restoration. The proportion of alien species remained stable in 96.8% of the projects

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Table 1. Results of generalized linear models on the effect of structural variables of the stream reaches and restoration projects on restoration outcomes. Data for variables are means (±1 SE) and p-values. Models were backward selected to the minimum Akaike Information Criterion (AIC_{min}). Rest. = restored. – = no data. Significant p-values are in bold.

Model	Abundance		Richness		Turnover		Diversity		Aliens	Endangered	
AIC_{min}	692.16		154.73		101.62		–58.61		202.77	291.60	
R^2_{adj}	0.13		0.53		0.19		0.36		0	0.06	
Variable											
River width	–		0.19 ± 0.05	**<0.001**	0.08 ± 0.03	**0.005**	–		–	0.28 ± 0.12	**0.030**
Restored length	–		–0.00 ± 0.00	0.13	–		–		–	–	
Catchment area	–		0.00 ± 0.00	**<0.001**	0.00 ± 0.00	0.07	0.00 ± 0.00	**0.047**	–	–	
Altitude	1.27 ± 0.42	**0.004**	–0.02 ± 0.00	**<0.001**	–		0.00 ± 0.00	**0.048**	–	0.02 ± 0.01	0.16
Age	–		–		–0.22 ± 0.09	**0.014**	–	**0.016**	–	–	

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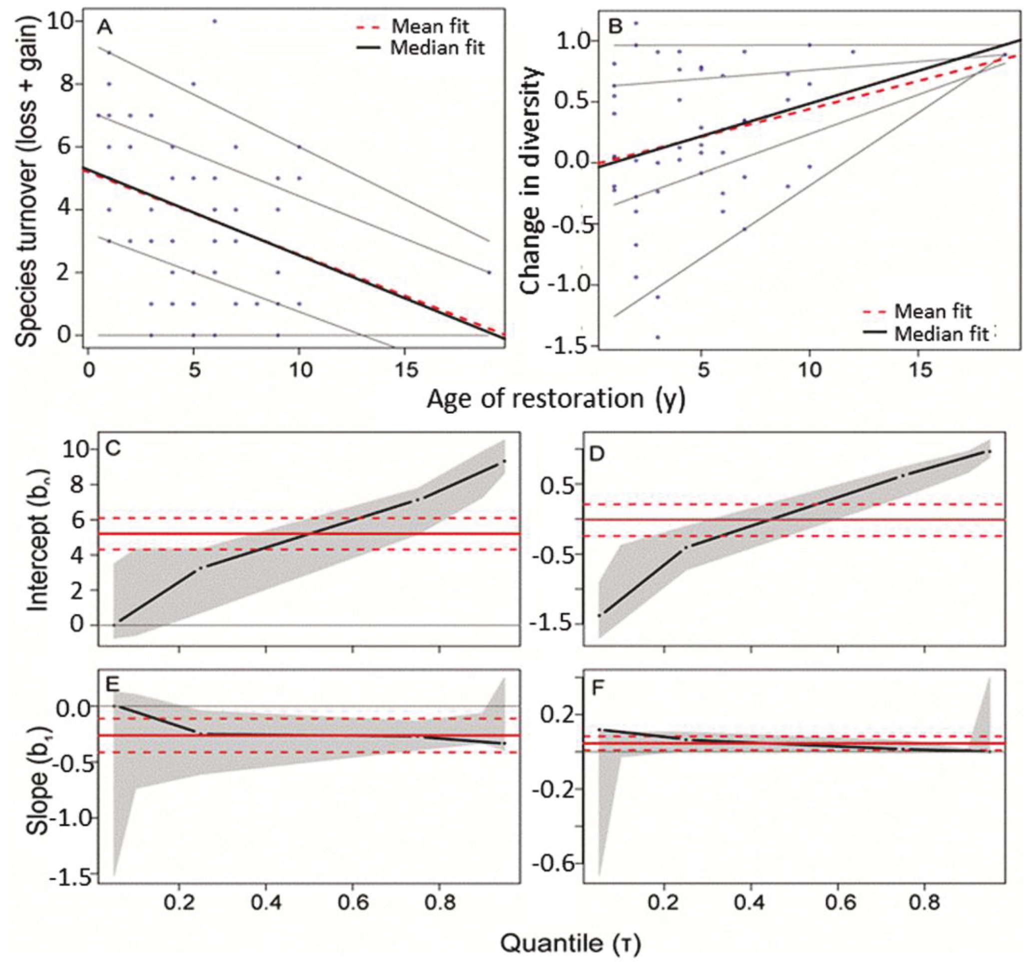

Figure 3. Quantile regression of median and linear regression of mean species turnover (A) and change in fish species diversity (B) as a function of the age of the restoration, and variation in intercepts (C, D) and slopes (E, F) for species turnover (C, E) and species diversity (D, F) regressions across the quantile ranges. Gray lines indicate regression lines for the quantiles τ = 0.05, 0.25, 0.75, and 0.95. Black lines and gray area give quantile estimates ± 95% confidence intervals, solid and hatched lines give least square esti mates ± SE.

(threshold = ±10%). An increase in alien species was observed in 1 project, and a decrease was observed on 1 other project (Fig. 2E). Endangered species were more variable (Fig. 2F) because more species were in this category. In most projects (63.0%), the abundance of endangered species remained almost unchanged. The number of projects in which endangered species abundance increased (22.2%) was slightly higher than those in which it decreased (14.8%). The proportion of endangered species that increased was greater in wider rivers. Changes in alien species were unrelated to stream characteristics (Table 1).

To summarize restoration effects at the community level, positive effects were observed for 3 of 5 metrics: species richness, abundance, and species diversity. Species turnover (metric 6) is neutral and cannot indicate whether an outcome is positive or negative. Of the 50 projects for which species richness, total abundance, and species diversity were calculated, 15 (30%) showed an increase in all 3 categories. No restoration project showed a decrease in all 3 categories.

Individual species responses

Forty-six fish species were found over all projects combined (Fig. 4). The 7 most abundant fish species that occurred in ≥½ of all projects were: *Salmo trutta m. fario*, *Squalius cephalus*, *Gobio gobio*, *Barbatula barbatula*, *Cottus gobio*, *Rutilus rutilus*, and *Gasterosteus aculeatus*. Almost half of all species (19) were rare and occurred in ≤5 projects.

Of the 21 species that occurred in ≥10 projects, 12 increased in abundance in ≥60% of the projects. These species included *Abramis brama, Alburnus alburnus*, *B. barbatula*, *Barbus barbus*, *C. gobio*, *Leuciscus leuciscus*, *Phoxinus phoxinus*, *P. parva*, *S. trutta m. fario*, *S. lucioperca*, *S. cephalus*, and *Thymallus thymallus* (Fig. 4). The species that most

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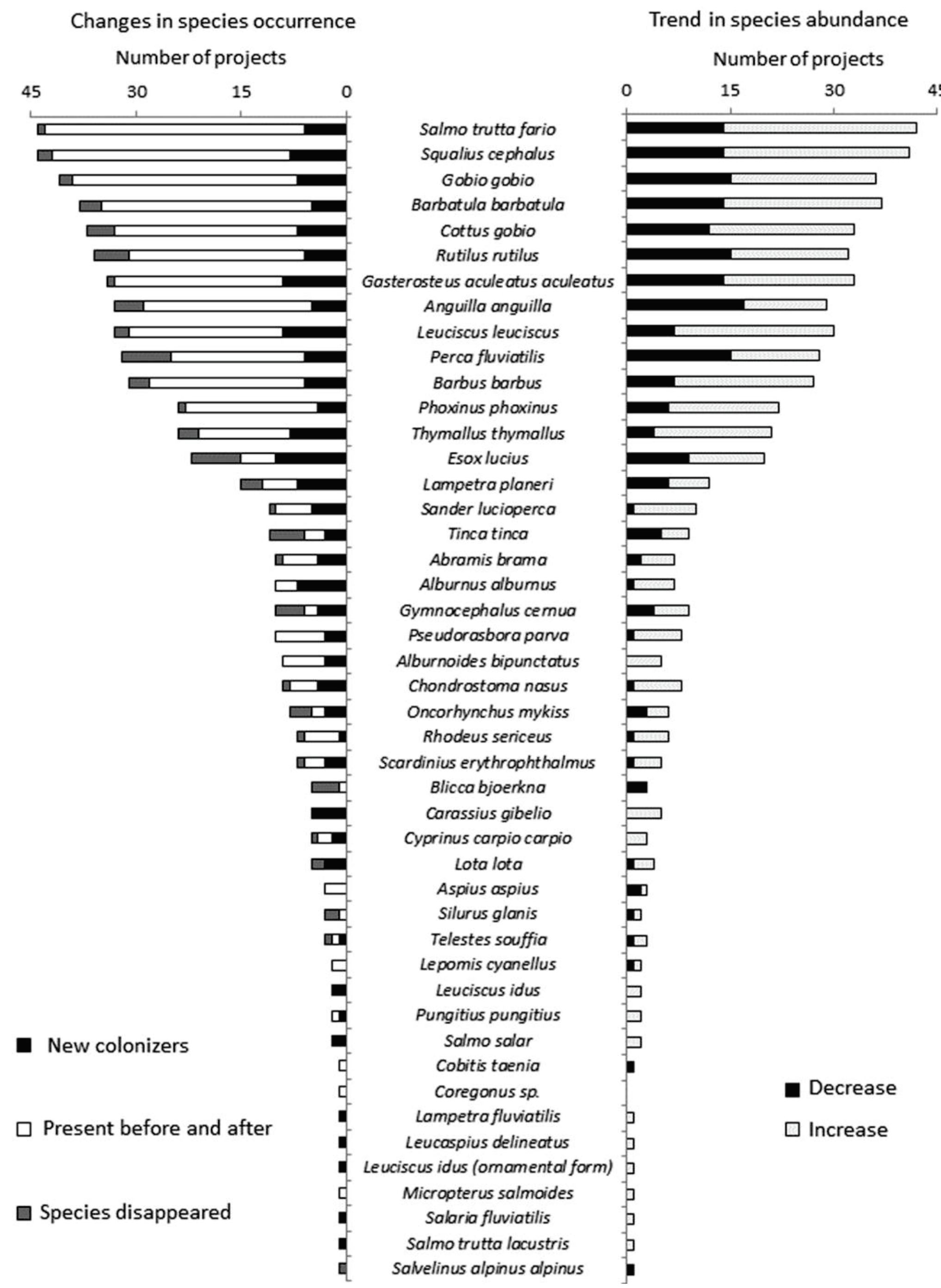

Figure 4. Changes in the occurrence and abundance of individual species in response to habitat restoration. The number of proj ects showing abundance might be smaller than for occurrence because abundance data were not available for all projects.

frequently declined in abundance was *Anguilla anguilla*, which declined in 59% of projects, followed by *Tinca tinca*, which declined in 55% of projects.

Six of the species that occurred in ≥10 restoration projects showed high colonization abilities with a positive net colonization rate >20%: *A. alburnus, A. brama, G. aculeatus, L. leuciscus, S. lucioperca*, and *T. thymallus* (Fig. 4). Three species showed a negative colonization balance and vanished from more projects than they colonized. These were: *Esox lucius, Gymnocephalus cernuus*, and *T. tinca.* In summary, *A. alburnus*, *L. leuciscus*, *S. lucioperca*, and *T. thymallus* benefited most from river restorations because they were most able to colonize restored reaches and to increase their abundance at sites where they had previously occurred. However, in some projects, these species vanished or decreased in abundance.

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Within the groups of functional traits, habitat preference showed the most distinctive response to habitat restoration (Fig. 5A, B). Compared to the overall mean, pelagic fish responded most positively in terms of occurrence and abundance. Fishes with pelagic–benthic habitat preferences showed only a slight improvement, and demersal fish increased in occurrence and abundance. Potamodromous fish decreased in abundance. The response within other functional groups was less pronounced. The occurrence of species with a phytophilic preference for reproductive habitat was polarized response with either disappearance or colonization events. Lithophilic species increased slightly in abundance, indicating that restoration improved breeding conditions in the interstitial zone.

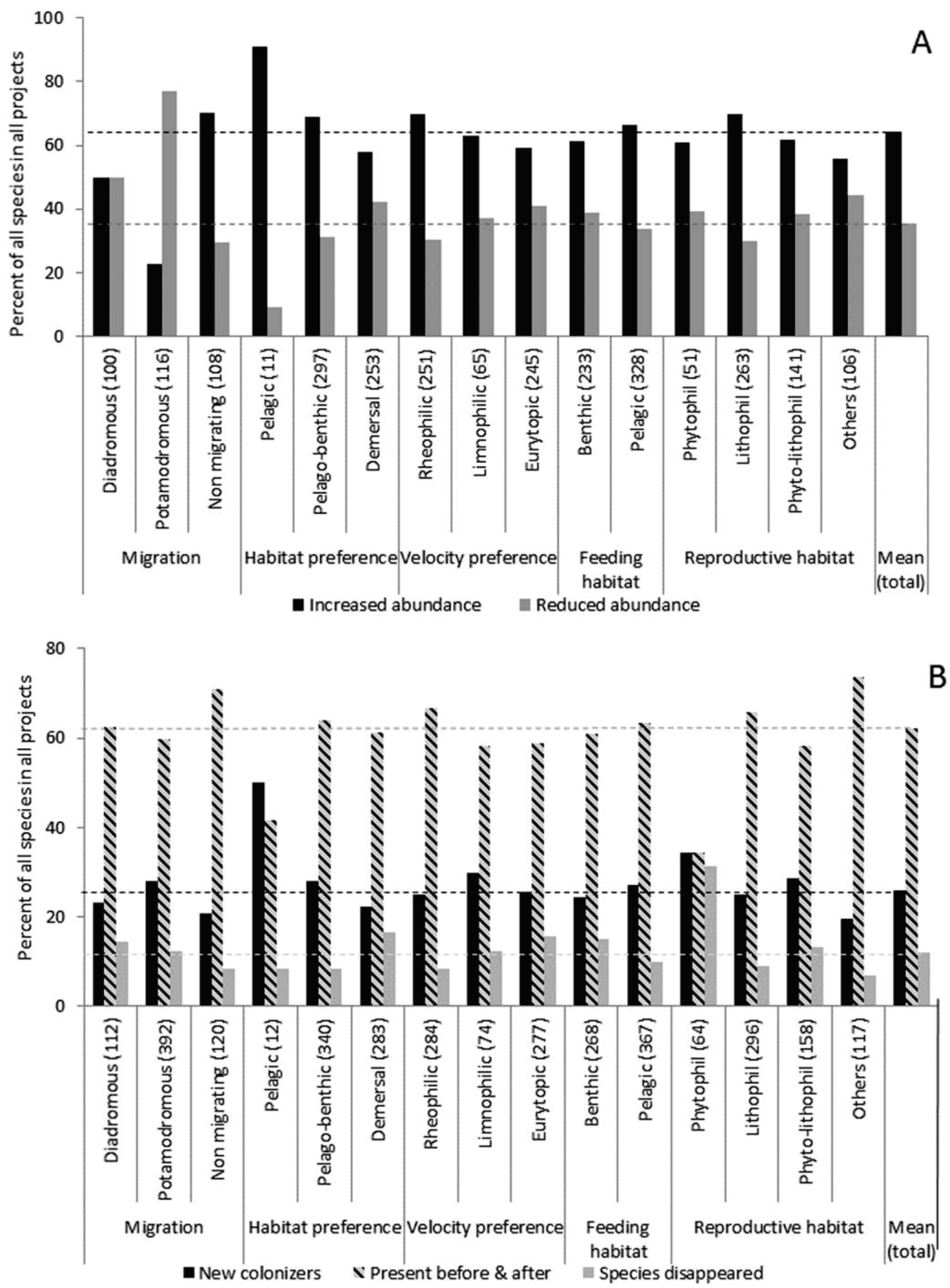

Figure 5. Changes in abundance (A) and occurrence (B) of fish grouped by functional traits in response to habitat restoration. Black and gray lines refer to the reference values of the mean fish response over all projects (bars labeled “mean total”). Bracketed numbers on the x axes indicate the sum of all species with the described trait over all projects.

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DISCUSSION

Community response to river restoration

Our analyses documented differences in fish community metrics, such as species richness, species diversity, and abundance resulting from river restorations. Most restoration projects featured a slight increase in species richness and diversity and a more pronounced increase in abundance. This general increase in fish abundance can arise by attraction of individuals to the restored habitats, increased survival, or enhanced recruitment success consequent to improved conditions (Gowan and Fausch 1996, Lorenz et al. 2013). Whiteway et al. (2010) analyzed salmonid responses in 211 habitat-restoration projects and found that abundance was enhanced significantly in 73% of projects. However, even though positive tendencies were visible in most projects, fish declined in richness, diversity, or abundance in some restored reaches compared to unrestored control reaches. Lorenz et al. (2013) showed that most of the increase in abundance was achieved by young-of-the-year fish, a result pointing to enhanced reproduction at restored reaches, whereas abundances of adult fish changed little. Furthermore, how far-reaching the observed changes were and to what extent natural fish composition was re-established by restoration techniques was unclear (Lorenz et al. 2013). Studies of a subgroup of restoration projects analyzed in our study revealed that fish communities regained natural reference condition in none of these projects (Haase et al. 2013, Stoll et al. 2013, 2014). Thus, the perceived success of restorations depends markedly on the endpoint against which success is evaluated (Jähnig et al. 2011).

Whether invasive species, which usually are habitat generalists (Marvier et al. 2004), can be pushed back by the restoration of structure-rich habitats that are more suitable for more specialized, native species is a matter of debate. Our results suggest that reach-scale river restoration is not a promising way to confine alien fish species. This conclusion is in line with that of Eros (2007), who found that nonnative species distribution was unrelated to habitat degradation when he analyzed fish species composition on a network scale at 158 sites in Hungarian streams. Likewise, we found no indication that alien species particularly benefited from river restorations. This finding is positive given contrasting predictions that restorations can act as disturbances in impaired environments and have the potential to promote alien freshwater fauna, at least in the initial phase (Kennard et al. 2005, Loo et al. 2009, Korsu et al. 2010).

Endangered fish showed much greater variation in response following restorations than alien species, but because the number of projects where endangered species were supported was only slightly higher than those in which they declined, we cannot conclude that restoration in general is beneficial for endangered species. Published literature reporting that river restoration successfully supports threatened freshwater fish species mostly originates from tailor-made restoration approaches, where constructed habitats were focused on the specific needs of these species, e.g., construction of riffle and pool sequences and cover habitats for a number of salmonid species (Bartz et al. 2006, Katz et al. 2007, Floyd et al. 2009). To strengthen endangered fish species sustainably, restoration and conservation efforts must be broadened over larger spatial scales than individual reaches to match the scale of the variables and processes that threaten these species in the first place (Labbe and Fausch 2000).

Community dynamics during recolonization phase

Our analysis revealed temporal dynamics for the metrics of fish community changes that were elicited by restoration. In the initial phase, high species turnover was observed. Species turnover declined and species richness remained constant with increasing age of the restorations, but changes in species diversity were more persistent and increased with the age of the restorations. Thus, after a few years, new species no longer colonize restored reaches, but the relative proportions of species present continue to change toward greater community evenness, which is reflected by increasing diversity indices (Stirling and Wilsey 2001). Restoration projects often are only the starting point for further ecological processes and habitat changes that continue to alter habitat for many years, e.g., after riparian reforestation. Acuña et al. (2013) estimated that 10 y are needed for restored riparian zones to begin providing dead wood to the stream channel. Therefore, we can expect species to adapt to habitat conditions that vary over time. Greater habitat complexity should increase species richness, and in consequence, foodweb complexity is expected to increase (Woodward and Hildrew 2002), which will allow more competitive species to persist in an environment of increased competition for resources.

Our finding that high species turnover was limited to the first years after restoration and then declined toward 0 allows another, more pessimistic view of the sustainability of the restored ecological processes. Initial change followed by reconvergence to the species composition of unrestored conditions might indicate that reach-scale restoration activities initially succeed in re-activating dynamic processes, but the initial benefit is lost within a few years because these processes typically are disturbed on a much larger spatial scale than the reach (Mayer and Rietkerk 2004). For example, reach-scale restorations might succeed in creating loose gravel beds that facilitate gravel-spawning fish recruitment for a couple of years, but if sediment input is not stopped at the catchment scale, these gravel beds will re-clog, leading to reduced success of gravel-spawning fish (Zeh and Donni 1994). With sparse data on older restorations, inferences on the long-term fate of restorations are equivocal, and we cannot conclusively identify which background process is causal for the reconvergence to the prerestoration species composition.

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In addition to the processes within restored reaches, the longitudinal connectivity of the entire stream system will influence recovery potential. Jansson et al. (2007) emphasized the role of free connectivity for the recovery process, especially when the dispersal abilities of species are limited. A study on fish kills after severe bushfires in Australia revealed that headwaters with a lower degree of cross-linking took longer to recover than did better cross-linked stretches further downstream (Lyon and O'Connor 2008). However, a well-connected stream system by itself will not guarantee ecological recovery if species have become extinct in entire subbasins and sources of recolonization are lacking. A study by Stoll et al. (2013) of a subset of restoration projects in the present study revealed that the vast majority of the species colonizing the restored reaches probably originated from immediately adjacent river reaches, whereas long-distance dispersal played only a minor role. Diebel et al. (2010) stated that undisturbed species pools in the immediate surroundings are a key factor in the ecological recovery of restored stream sections. The importance of connectivity and species pools in the surrounding reaches also has been emphasized by Hughes (2007).

Most studies of recovery times of freshwater communities after disturbance conclude that recovery occurs within few years because: 1) the life-history characteristics of the species involved allowed rapid recolonization and repopulation; 2) refugia within, up-, or downstream of the affected reach act as sources for recolonization; 3) in cases of pulse-disturbances that affect water quality, the flow guarantees a fast exchange of harmful conditions; and 4) lotic systems are naturally prone to disturbance events, and therefore, biota have evolved to cope with these unstable conditions (Niemi et al. 1990, Yount and Niemi 1990). Recovery after disturbances also has a spatial component. Shorter reaches are recolonized more quickly than long river sections. Because the spatial dimensions of habitat-restoration projects commonly are in the range of several hundred meters to very few kilometers, we should expect fast colonization.

Reviews and meta-analyses of recovery times following stream restorations are scarce. An analysis of various indicators of ecological success for 41 river-restoration projects in Germany, Britain, and The Netherlands (Matthews et al. 2010) showed no temporal pattern in short-term rehabilitation within the first 5 y after the restorations were completed. The lack of a time effect between 1 to 5 y after a restoration indicates that initial colonization occurred within a year, but the time period investigated was too short to detect long-term processes occurring at a slow pace. Moreover, long-term processes can be obscured by superimposed stochastic effects. Schmutz et al. (2013) found that density of rare species increased, whereas the number of rare species and density of other species declined over time at restored sites (n = 19) evaluated 0.5 to 6 y after restoration in the Danube. The only publication we found that covered much longer recovery times was by Trexler (1995), who estimated that in the Kissimmee River, Florida (USA), where a large-scale restoration project was carried out, fish required 12 to 20 y to make a full recovery. Much longer recovery times can be expected for restored ecosystems when 'species composition' measures the functionality of restored processes, such as recruitment success and survival or mortality, over larger time-scales rather than just the ability of restored reaches to attract dispersing individuals. Responses to restored functionality (e.g., spawning grounds, nursery habitats, or shading by riparian vegetation) might take much longer to manifest and will depend on the life-history traits (e.g., age of maturity or development times) of the colonizers. However, studies of the long-term (>20 y) effects of restoration projects are rare (e.g., see Parkyn et al. 2003), particularly because only a few restorations have reached this age.

Effects of spatial environmental gradients on restoration outcomes

Recovery dynamics might differ over large spatial scales because species richness and diversity typically decline toward the headwaters (Eros 2007, Troia and Gido 2013). Fukami and Wardle (2005) stated that natural and anthropogenic gradients must be considered when assessing ecological dynamics. Our analyses showed that species richness and changes in species diversity at restored reaches were positively related to river width and upstream catchment size. Other metrics including species turnover, abundance, and changes in the proportion of endangered or non-native species depended much less or not at all on such natural gradients. Within the set of reach-scale restorations that we studied, the actual length of restored sections did not affect the restoration outcome. If the results we observe are driven mainly by dispersal from the immediately adjacent surrounding reaches, we should not be surprised that restored length was not important for recovery because none of the projects we evaluated was done on a catchment scale. However, if restoration were broadened to include whole river branches or catchments, entire ecological processes might be restored. In contrast, Schmutz et al. (2013) found a positive correlation between rheophilic fish and restored stream length at 0.05 to 9.7-km-long restored sites in the Danube, suggesting that the spatial extent of restorations in large rivers needs to be >3.9 km. Such large-scale recovery processes may lead to different outcomes. Hypothetically, in such a situation, dispersal would be a first step in recolonization, but successful recruitment and survival might further alter fish species composition later as spawning and nursery habitats become established and processes continue to be dynamic. This situation was observed in large-scale river-restoration projects completed in Denmark (Feld et al. 2011).

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Response of individual species and relationship to ecological species traits

The dispersal and competitive abilities of species are expected to drive the dynamics of the colonization process. Therefore, a more detailed view of individual species responses may help inform general conclusions and provide an indication of which species might benefit from habitat restorations. *Alburnus alburnus*, *T. thymallus*, *L. leuciscus*, and introduced *S. lucioperca* consistently responded positively to the restorations. However, *T. thymallus* and *S. lucioperca* are key species of angling interest, and we cannot rule out the possibility that, in some cases, the positive response might have been enhanced by stocking. Stocking probably is not a concern for species of no angling interest, such as *A. alburnus* and *L. leuciscus*. The negative response of *A. anguilla* after restoration probably is caused by the loss of artificial habitats, such as rip-raps and other bank-stabilization structures, commonly occupied by this species (Lasne et al. 2008).

Examination of responses of species groups defined on the basis of their functional traits revealed a trend within the habitat-preference group. Pelagic fish benefited more than demersal fish from restoration. At first glance, this result seems surprising because an increase in habitat complexity should benefit those species that show a stronger linkage to in-stream structures. On the other hand, most demersal species are poor swimmers and would be expected to disperse slowly. Pelagic fish are better swimmers and, therefore, are more likely to disperse into restored reaches and establish themselves. Furthermore, pelagic species might benefit from increased heterogeneity in velocity because rheophilic species also showed a slight increase in abundance. This trend is in line with findings by Schmutz et al. (2013), who found that rheophilic species performed better than limnophilic species at 19 restoration sites in the Danube. The increase in abundance of lithophilic species in the reproductive-habitat group may arise from improved recruitment conditions, e.g., loosening or addition of gravel and establishment of shallow marginal habitats (Lorenz et al. 2013). The polarized response of phytophilic fishes may be an indirect result of macrophyte response to habitat restorations. Lorenz et al. (2012) showed that macrophytes respond positively to habitat restoration, so phytophilic fishes may have benefited from the macrophyte recovery. The declining abundance of potamodromous fish is probably not related to restoration efforts, but rather displays the overall declining trend of migratory species suffering from fragmentation of riverine ecosystems over large spatial scales (Freeman 2003).

Conclusion

The results of our meta-analysis demonstrate that fish communities were positively affected in most reach-scale restorations aimed at overall hydromorphological improvement of rivers. Fish abundance, and to a lesser extent, species richness and diversity increased, whereas negative effects were negligible. Nevertheless, historic reference conditions for fish communities have not been achieved. Reach-scale river restorations can be considered a useful management tool to support local fish communities. However, the lack of effects on endangered species emphasizes that habitat-restoration techniques chosen for conservation reasons should include strategies and techniques directed at the species of interest. The return of communities to unrestored conditions suggests that degradation processes are still present at larger spatial scales. Such large-scale pressures on riverine systems should be considered during planning to ensure sustainable restoration effects. Last, the temporal dynamics of community composition indicates that a final evaluation of restoration outcomes is not feasible in the first years after completion of restoration, but that fish communities undergo a succession process from rapid colonizers to more competitive species. Repeated samplings of species communities and habitat structure in restoration projects over prolonged periods would help clarify the sustainability of recovery in reach-scale restoration projects and improve understanding of the dynamics of species recovery.

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