Diverging response patterns of terrestrial and aquatic species to hydromorphological restoration

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Abstract: *Although experiences with ecological restoration continue to accumulate, the effectiveness of restoration for biota remains debated. We complemented a traditional taxonomic analysis approach with information on 56 species traits to uncover the responses of 3 aquatic (fish, macroinvertebrates, macrophytes) and 2 terrestrial (carabid beetles, floodplain vegetation) biotic groups to 43 hydromorphological river restoration projects in Germany. All taxonomic groups responded positively to restoration, as shown by increased taxonomic richness (10–164%) and trait diversity (habitat, dispersal and mobility, size, form, life history, and feeding groups) (15–120%). Responses, however, were stronger for terrestrial than aquatic biota, and, contrary to our expectation, taxonomic responses were stronger than those of traits. Nevertheless, trait analysis provided mechanistic insights into the drivers of community change following restoration. Trait analysis for terrestrial biota indicated restoration success was likely enhanced by lateral connectivity and reestablishment of dynamic processes in the floodplain. The weaker response of aquatic biota suggests recovery was hindered by the persistence of stressors in the aquatic environment, such as degraded water quality, dispersal constraints, and insufficient hydromorphological change. Therefore, river restoration requires combined local- and regional-scale approaches to maximize the response of both aquatic and terrestrial organisms. Due to the contrasting responses of aquatic and terrestrial biota, the planning and assessment of river restoration outcomes should consider effects on both components of riverine landscapes.*

Keywords: functional diversity, multibiotic diversity, riparian, river floodplain, stream restoration, taxonomic composition, trait composition

Patrones Divergentes de Respuesta de las Especies Terrestres y Acuáticas ante la Restauración Hidromorfológica

Resumen: *Aunque se siguen acumulando las experiencias con respecto a la restauración ecológica, la efectividad de la restauración para la biota todavía está en discusión. Complementamos un método de análisis taxonómico tradicional con información sobre 56 rasgos de especies para descubrir las respuestas de tres grupos bióticos acuáticos (peces, macroinvertebrados, macrofitas) y dos grupos bióticos terrestres (escarabajos carábidos, vegetación de planicies inundables) ante 43 proyectos de restauración hidromorfológica de ríos en Alemania. Todos los grupos taxonómicos respondieron positivamente a la restauración, como lo demostró el incremento en la riqueza taxonómica (10-164%) y en la diversidad de rasgos (hábitat, dispersión y movilidad, tamaño, forma, historia de vida, y grupos de alimentación) (15-120%). Sin embargo, las respuestas fueron más fuertes para la biota terrestre que para la acuática, y, contrario a nuestra expectativa, las respuestas taxonómicas fueron más fuertes que las respuestas de los rasgos. Aun así, el análisis de los rasgos proporcionó conocimiento mecánico sobre los conductores del cambio comunitario tras la restauración. El análisis de los*

rasgos para la biota terrestre indicó que el éxito de la restauración probablemente estaba mejorado por la conectividad y el restablecimiento de los procesos dinámicos en la planicie inundable. La respuesta más débil de la biota acuática sugiere que la recuperación estuvo obstaculizada por la persistencia de las fuentes de estrés en el ambiente acuático, como la calidad degrada del agua, las restricciones de dispersión, y el cambio hidromorfológico insuficiente. Por lo tanto, la restauración de ríos requiere estrategias de restauración de ríos locales y regionales combinadas para maximizar la respuesta tanto de los organismos terrestres como de los acuáticos. Debido a las respuestas contrastantes entre la biota terrestre y la acuática, la planeación y la evaluación de los resultados de la restauración de ríos debería considerar los efectos sobre ambos componentes de los paisajes ribereños.

Palabras Clave: composición de rasgos, composición taxonómica, diversidad funcional, diversidad multibiótica, planicie inundable ribereño, restauración de corriente, ribereño

Introduction

In recent years, billions of dollars have been invested in ecological restoration to mitigate global change effects and slow down the rate of biodiversity loss (Holl & Howarth 2000). Yet, restoration project outcomes are too often not, or inconsistently, evaluated (Bernhardt et al. 2005). Where assessments have been performed, the effectiveness of restoration has depended on the intensity of restoration measures, landscape settings, chosen response targets, and evaluation design (Palmer et al. 2010; Kail et al. 2015).

As neighboring ecosystems are generally strongly linked, restoration is likely to benefit more than the target ecosystem. Thus, it is surprising that cross-ecosystem effects of restoration are rarely considered by evaluation plans. A prime example is rivers and their floodplains, which are strongly interconnected (Hjältén et al. 2016) through processes such as sediment dynamics, nutrient inputs, reciprocal food-web subsidies, and by organisms spending their life cycle in both ecosystems (Schulz et al. 2015). Therefore, restoration measures implemented within the river channel may also affect the adjacent floodplain ecosystem, and vice versa. However, evaluations of the response of biota to river restoration traditionally focus on aquatic-only or terrestrial-only taxonomic groups (see e.g., meta-analyses synthesizing the outcomes of several [91 and 211] projects for aquatic organisms [Whiteway et al. 2010; Kail et al. 2015]). Only in a few cases have aquatic and terrestrial biota been studied simultaneously (Jähnig et al. 2009; Januschke et al. 2014; Hering et al. 2015; Nilsson et al. 2017; Turunen et al. 2017; Lorenz et al. 2018), and these were mostly restricted to a limited number of rivers (≤10 rivers within 1 or 2 catchments) and taxonomic groups.

Because different taxonomic groups respond to different suites of drivers and constraints that act at different spatial and temporal scales (Tockner et al. 1999), analyzing their joint responses to restoration is important to further understanding of the effectiveness of restoration (Lorenz et al. 2018). Such a cross-taxa examination requires approaches that go beyond taxonomy. Community-wide functional traits are one

such tool that can increase our understanding of complex ecological patterns (Dolédec et al. 1999; Tolonen et al. 2016). Traits have the potential to suit multibiotic studies, where trait responses by different taxonomic groups can shed light on key ecological processes and balance the bias caused by the different species richness. Therefore, a comprehensive evaluation of river restoration projects through a combination of multiple aquatic and terrestrial taxonomic groups and their functional traits can provide insights into the overall effectiveness of restoration and the possible constraints to biotic recovery and provide key indications for effective management.

We combined taxonomic- and trait-based analyses for a multibiotic and cross-ecosystem evaluation of hydromorphological restoration of rivers. We analyzed the response of three aquatic (fish, macroinvertebrates, macrophytes) and 2 terrestrial (carabid beetles, floodplain vegetation) taxonomic groups to 43 river restoration projects in Germany, by comparing taxonomic and trait diversity and composition between paired restored and unrestored (impacted) reaches. We analyzed a large set of traits ($n = 56$) describing habitat preferences, dispersal and mobility, organism size and form, life history and reproduction, and, for animals, feeding groups. We hypothesized that restoration affects trait diversity and composition more than taxonomic richness and composition because traits reflect the community adaptation to abiotic changes and are less affected by stochastic factors (Townsend & Hildrew 1994), and that restoration affects terrestrial biota more than aquatic biota because the recovery of terrestrial biota is less constrained by persisting stressors after restoration (e.g., longitudinal fragmentation and water pollution) (Jähnig et al. 2009; Lorenz et al. 2018).

Methods

Study Area and Approach

We sampled 43 different restoration projects in Germany (Supporting Information), for fish (31 projects), macroinvertebrates (36 projects), macrophytes (37 projects), riparian carabid beetles (36 projects), and

floodplain vegetation (35 projects). A subset of 21 projects was surveyed where all the studied taxonomic groups were examined together. The restoration projects were implemented between 1988 and 2012 and aimed at improving the hydromorphological structure (39 projects) and/or flood protection (17 projects) and/or river continuity (13 projects) and involved different combinations of nine restoration methods (Supporting Information). Surveys were conducted from 2005 to 2014, once for each project; project age ranged from 1 to 26 years. For each project, a restored reach and an adjacent impacted control reach, which represented the conditions of the restored site prior to restoration, were surveyed. Generally, the control reach was located upstream of the restored reach, except for eight projects (Supporting Information), where it was located downstream for technical reasons, for example, presence of a waste water treatment at short distance upstream of the restored site. Throughout the study we applied a pairwise approach, comparing biotic metrics between the restored and the adjacent control reaches. We synthesized the responses of the 5 taxonomic groups by applying a uniform approach of taxonomic and trait analysis. The analysis of the hydromorphological changes between restored and control reaches is reported in Supporting Information.

Data Collection

The 5 taxonomic groups were sampled following standardized protocols (Supporting Information, Appendix B). Overall our dataset included 36 fish taxa, 183 macroinvertebrate taxa, 95 macrophyte taxa, 125 carabid beetle taxa, and 470 floodplain vegetation taxa.

TRAITS

We gathered trait data for the 5 taxonomic groups from the literature and grouped traits describing habitat preferences, dispersal and mobility, organism size and form, life history and reproduction, and feeding group for animals only (Supporting Information). These trait groups were selected based on their likely response to restoration and their coverage in the literature for the 5 taxonomic groups. Habitat preference traits may indicate increased preferences for wetter habitats for terrestrial groups, and increased diversity for aquatic and terrestrial groups, reflecting enhanced habitat heterogeneity. Dispersal and mobility traits may indicate increased abundance of strong dispersers following restoration, reflecting their ability to reach new habitats, greater prevalence of hydrochory (for floodplain vegetation and macrophytes) and species dispersing by downstream drift (macroinvertebrates), due to increased channel retention capacity. Organism size and form traits can reveal tolerance to disturbance. Life history and reproduction traits may

exhibit a change toward more opportunistic characters (e.g., short life span and abundant offspring) in the first years after restoration, which would favor the colonization of free niches in newly created habitats. Functional feeding traits can inform about changes in the food base (e.g., higher heterogeneity of food resources may promote aquatic diversity), and aquatic-terrestrial coupling, which may promote predatory terrestrial carabid beetles.

The trait data set included 12 traits (42 modalities) for fish, 12 traits (61 modalities) for macroinvertebrates, 13 traits (35 modalities) for macrophytes, 6 traits (19 modalities) for carabid beetles, and 13 traits (29 modalities) for floodplain vegetation (Tables S4 and S5 in Supporting Information). We scaled each trait from 0 to 1 to ensure equal weight across traits.

We used the function functcomp in the R package FD to compute the trait composition for each taxonomic group at each studied reach as the mean trait-modality values of all taxa present in the community weighted by their relative abundances (Laliberté & Shipley 2014).

Data Analyses

We computed taxonomic richness and overall trait diversity (including all the studied traits) for each study reach and each taxonomic group. We calculated taxonomic richness as the total number of taxa in the community and the overall trait diversity as the convex hull volume occupied by the community in the multidimensional trait space (Villéger et al. 2008). We included all the studied traits for which we found information for >80% of the studied taxa (Supporting Information). For the computation of trait diversity, we used the dbFD function in the R package FD (Laliberté & Shipley 2014). We standardized the values of trait diversity by the global diversity that included all species so that values were from 0 to 1.

We then compared the differences in the values of taxonomic richness and trait diversity between control and restored reaches with a pairwise Wilcoxon signed-rank test because of violation of parametric pairwise t test assumptions. We computed the effect size as Cohen´s D (Cohen 1988).

We tested whether taxonomic and trait composition significantly differed between paired control and restored reaches with permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001), which we performed using the adonis function in the R package vegan (Oksanen et al. 2013). Reach type (control or restored) was the fixed factor and river was the strata. If the design is balanced, as in our case, PERMANOVA is robust even when the spread among groups differs (Anderson & Walsh 2013). We used Bray-Curtis dissimilarity on taxon abundances, which were $\log(x+1)$ transformed, and on trait composition data. We computed the extent of the

changes in community composition as the averaged pairwise community (Bray-Curtis) dissimilarity of each paired restored and control reach for each taxonomic group.

To identify the traits most sensitive to restoration, we computed the trait diversity for each group of traits and each taxonomic group, following the approach described above for the overall trait diversity. We then compared the differences in the values of each trait modality and richness metric between control and restored reaches with pairwise Wilcoxon signed-rank tests and applied Bonferroni's correction of significance levels to account for multiple comparisons within each trait group.

Our data set included a variety of river types and restoration projects that had different spatial extents and were 1–26 years old. We tested whether such factors influenced the results by running, for each biotic group, linear models with effect sizes for the studied biotic metrics (differences in taxonomic richness and trait diversity and dissimilarity in taxonomic and trait composition between control and restored reaches) as response variables and catchment area, length of the restored reach, and restoration age as explanatory variables. We log transformed the variables when necessary to satisfy normality assumptions. We performed stepwise model selection based on Akaike information criterion with the function stepAIC in the R package MASS (Venerables & Ripley 2002). Moreover, we analyzed nonlinear relationships between the effect sizes of the studied biotic metrics and trait modalities and restoration age with additive models (gam function in the R package mgcv [Wood 2011]).

Results

Restoration led to an increase in physical complexity at restored reaches relative to control (affected) reaches, and similar positive effects occurred in aquatic and terrestrial habitats. However, neither aquatic nor floodplain environments reached complexity levels that could resemble those of rivers in undisturbed conditions (Supporting Information).

Taxonomic Richness and Composition

Taxonomic richness was significantly higher at restored than control reaches for all the studied taxonomic groups; effects were 82% stronger on terrestrial than on aquatic biota (Fig. 1a,b). On average, we recorded an increase of 1 fish taxon (22%), 2 macroinvertebrate (10%), 3 macrophyte (67%), 5 carabid beetle (164%), and 22 floodplain vegetation (62%) taxa at restored reaches compared with control (affected) reaches. Similarly, the differences in taxonomic composition between control and restored reaches were 85% higher for the terrestrial biota (significant for both carabid beetles and floodplain

vegetation) than for the aquatic biota, for which significant differences were recorded only for macrophytes (Fig. 1a, Table 1, & Supporting Information). Restoration age and length of the restored reach had no significant effects on the changes in taxonomic richness and composition ($p > 0.05$). Changes in taxonomic richness of fish ($R^2 = 0.12$, $F = 5.17$, df = 1 and 20, $p = 0.030$) and carabid beetles ($R^2 = 0.14$, $F = 6.69$, df = 1 and 34, $p = 0.014$) were positively correlated with catchment area.

Trait Diversity and Composition

Overall trait diversity was higher at restored than at control reaches for all taxonomic groups (statistically significant, $p < 0.05$, for all groups except carabid beetles) (Fig. 1a, Table 1, & Supporting Information); average increase was 15% for fish, 166% for macroinvertebrates, 367% for macrophytes, 47% for carabid beetles, and 120% for floodplain vegetation. The average effect size for trait diversity was similar for aquatic and terrestrial biota (Fig. 1b). Differences in the overall trait composition between control and restored reaches were 63% higher for the terrestrial biota (significant for carabid beetles and floodplain vegetation, $p < 0.05$) than for the aquatic biota (no significant differences for any group) (Fig. 1a & Table 1). Restoration age and length of the restored reach had no significant effects on trait diversity and composition ($p > 0.05$). Catchment area was positively correlated to the changes in trait composition of fish ($R^2 = 0.11$, $F = 4.75$, df = 1 and 30, $p = 0.037$) and carabid beetles ($R^2 = 0.10$, $F = 5.03$, df = 1 and 34, $p = 0.031$), and negatively correlated to the changes in trait composition of macrophytes ($R^2 = 0.19$, $F = 9.32$, df = 1 and 35, $p = 0.019$).

The increases in trait diversity and the changes in the relative abundance of trait modalities within the studied groups of traits (habitat preferences, dispersal and mobility, organism size and form, life history and reproduction, and feeding groups) at restored reaches were stronger and more consistent for terrestrial than aquatic biota (Fig. 2). Specifically, we found increases in diversity or changes in the relative abundance of trait modalities for all trait groups for the terrestrial biota (carabid beetles and floodplain vegetation) and for macrophytes. For the other aquatic groups, we found only an increase in abundance of fish species spawning on sand habitats and a higher diversity of traits describing dispersal and mobility for macroinvertebrates at restored reaches. Restoration age had no significant effects on trait modalities ($p > 0.05$).

Discussion

Our multibiotic, cross-ecosystem study revealed that all 5 taxonomic groups benefitted from the increased physical complexity following restoration in both the
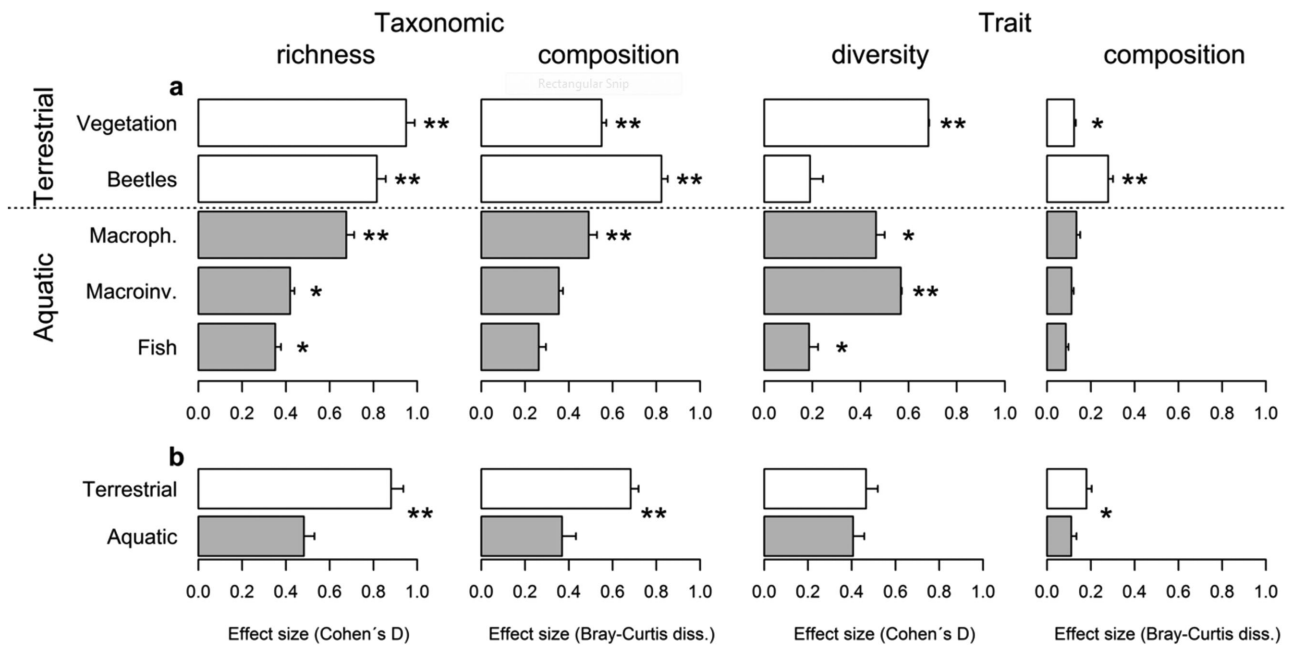
Figure 1. Effect of river restoration on (a) taxonomic richness and composition and trait (habitat, dispersal and mobility, size, form, life history and reproduction, and feeding groups) diversity and composition and (b) averaged restoration effect-size values for terrestrial and aquatic groups. Differences between paired restored and control reaches reported as effect sizes (Cohen's D and SE) of the mean differences for taxonomic richness and trait diversity and as mean Bray-Curtis dissimilarity (and SE) for taxonomic and trait composition (*, $p < 0.05$, **, $p < 0.01$).

Table 1. Comparison of biotic metrics between paired restored and control river reaches based on pairwise Wilcoxon signed-rank test for taxonomic richness and trait diversity and PERMANOVA for taxonomic and trait composition.*

	Taxonomic richness		Trait diversity		Taxonomic composition		Trait composition	
Metric	V	p	V	p	pseudo-F	p	pseudo-F	p
Vegetation	618.5	<0.001	587.00	<0.001	1.80	0.001	1.84	0.043
Beetles	525.5	<0.001	412.00	0.220	3.61	0.001	13.51	0.001
Macrophytes	474.50	<0.001	488.00	0.015	1.30	0.004	1.01	0.214
Macroinv.	459.50	0.018	526.00	0.002	0.41	0.238	0.51	0.180
Fish	294.00	0.038	329.00	0.048	0.28	0.236	0.41	0.063

* *Number of paired reaches: fish, 31; macroinvertebrates, 36; macrophytes, 37; carabid beetles, 36; floodplain vegetation, 35.*

river channel and the floodplain area. However, aquatic biota showed weaker responses to restoration than terrestrial biota, which confirmed our expectations. Contrary to our first hypothesis, taxonomic responses were stronger than those of traits. Increases in taxonomic richness and changes in taxonomic composition were not systematically followed by increases in trait diversity and changes in trait composition.

According to a general ecological assumption, increased physical heterogeneity is associated with higher biodiversity through a greater availability of potential niche space for multiple species with different ecological requirements than homogeneous environments (MacArthur 1965). Although this may apply to natural settings (Beisel et al. 2000; Passy & Blanchet 2007), restoration of degraded environments does not always succeed

in enhancing biodiversity (Palmer et al. 2010), mainly due to the overriding effects of remaining stressors that prevent species recolonization. Successful cases exist (Miller et al. 2010; Verdonschot et al. 2016; Pilotto et al. 2018), however, and their results are consistent with ours that indicate the increased breadth of habitat conditions produced by restoration in degraded rivers allowed for the establishment of richer communities with more diverse trait combinations for all studied taxonomic groups.

Taxonomic and Trait Patterns

The comparisons of significant changes in taxonomic richness and trait diversity on the one hand and taxonomic composition and trait composition on the other
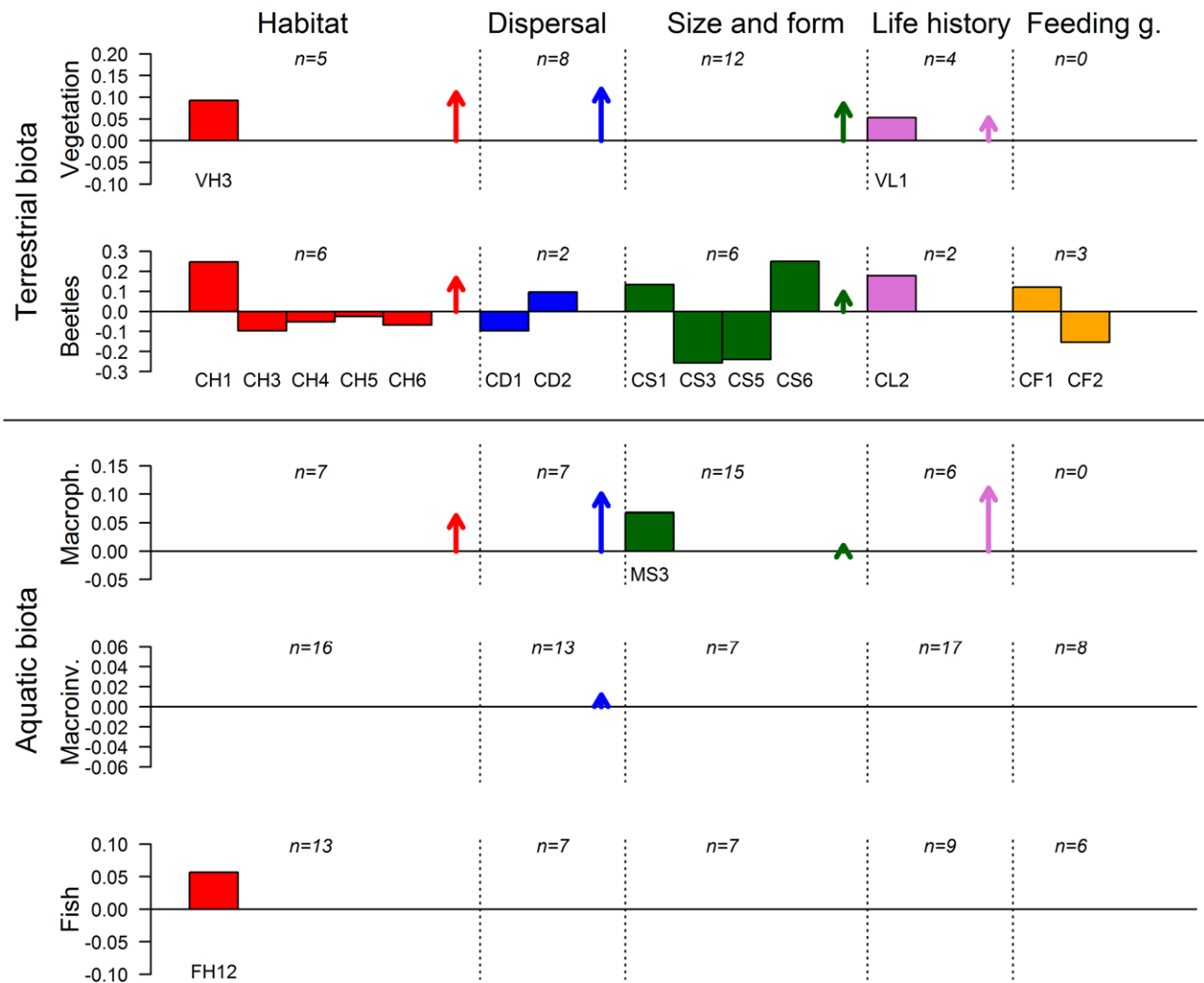
Figure 2. Mean differences in trait-modality values (bars) and trait richness (arrows) between paired restored and control river reaches for 5 taxonomic groups and 5 groups of traits (n, total number of trait modalities tested per biotic metric and trait group; F, fish; C, carabid beetles, M, macrophytes; V, vegetation; FH12, reproduction habitat, psammophilic; MS3, elodeid; CH1, riparian and floodplain areas; CH3, forest; CH4, dry areas; CH5, immature soils; CH6, agricultural areas; CD1, hind wing, brachyptera; CD2, hind wing, macroptera; CS1, small body; CS3, large body; CS5, medium size eyes; CS6, large eyes; CL2, overwintering stage, imago; CF1, predator; CF2, herbivore; VH3, Ellenberg moisture; VL1, life span annual). Only significant (p < 0.05) trait modalities and richness differences between the 2 reach types are shown. A full list of traits and modalities is in Supporting Information. The y-axes differ.

hand resulted in identical patterns in 8 of 10 comparisons and indicated similar responses by taxonomic- and trait-based analyses. The remaining 2 comparisons indicated a slightly stronger taxonomic signal. Indeed, the changes in taxonomic composition were not mirrored by significant changes in trait composition for macrophytes. We do not have a clear explanation of that pattern but we can speculate that it may be due to a certain degree of functional redundancy (Rosenfeld 2002). Increased taxonomic diversity did not result in a significant increase in trait diversity for carabid beetles, which might depend on the fact that carabid beetles are from only 1 family,

therefore their overall potential trait diversity is limited compared with the other taxonomic groups that are much more taxonomically differentiated (i.e., including several families). The large differences in trait composition between control and restored reaches, however, suggest that the carabid beetle communities shifted from terrestrial habitat specialists to more river and floodplain habitat specialists.

Although the trait-based approach showed weaker responses to restoration than the taxonomic-based approach, it provided mechanistic insights into the drivers of community change following restoration.

This is particularly true for the 2 terrestrial groups. We recorded an increased abundance of hydrophilic floodplain vegetation and riparian-specialist carabid beetles after restoration. This increase may have been driven by the enhanced lateral connectivity between the river channel and the floodplain (Januschke et al. 2011; Modrak et al. 2017) after the implementation of planform restoration methods (rebraiding and removal of bank fixations), which can increase the frequency and duration of inundations (Jähnig et al. 2009). Maintaining floods is crucial for floodplain vegetation (Tonkin et al. 2018b) and the formation of dynamic riparian habitats is essentials for carabid beetles (Januschke & Verdonschot 2016).

Enhanced lateral connectivity and increased frequency and duration of inundations usually lead to an increased availability of differentiated habitat niches (Tonkin et al. 2018b). Associated with this enhanced lateral connectivity, we found an increased diversity in growth forms and life history traits for floodplain vegetation at restored reaches. Annual floodplain plant species were also in greater abundance compared with longer-lived species, which could indicate an adaptation to cope with physical disturbances (Göthe et al. 2016) induced by the restoration, both via the physical restoration itself (e.g., through the use of heavy machinery in the riparian zone), and the more frequent flooding events (Hasselquist et al. 2015). However, in the former case we would expect a decline of such traits modalities with increasing restoration age, which we did not track despite the large range of ages that was covered by the studied projects (1 to 26 years). Thus, the increased adaptation to disturbed environments is likely a response to the increased flood disturbance at restored reaches (Göthe et al. 2016), which would further indicate that restoration succeeded in increasing lateral connectivity. At restored reaches, the diversity of carabid beetle size and form also increased as did a trend toward smaller species with larger eyes and abundance of predator taxa. These trends were mainly driven by the high abundances of the small predator *Bembidion* species, which prevails on open gravel bars frequently generated by restoration (Januschke & Verdonschot 2016), further indicating the success of planform changes.

Response Pattern of Terrestrial and Aquatic Biota

Aquatic biota showed weaker responses to restoration than terrestrial biota, which confirms the findings of previous work (Jähnig et al. 2009; Lorenz et al. 2018) and supported our second hypothesis. One reason for this might be an ongoing catchment-wide water quality impairment, which the studied restoration projects did not address (restoration was focused on hydromorphology), and may still impair the recovery of aquatic biota and weaken their response to restoration (Leps et al. 2016). Indeed, the large majority of studied rivers do not meet the quality criteria defined by the EU Water Framework

Directive (2000/60/EC) for river basin-specific pollutants (83%, data available for 36 rivers), physicochemical quality elements (83%, data available for 35 rivers), and priority substances (82%, data available for 38 rivers; without Hg: 38%; data available for 21 rivers; data retrieved from the water authorities of the German federal states).

By contrast to the above reported community changes for terrestrial biota, the aquatic biota did not show significant changes in trait composition at restored reaches. Moreover, for fish and macroinvertebrates we could not track any increase in habitat-trait diversity, in the heterogeneity of organism size, form, and feeding traits, or a prevalence of opportunistic traits, not even in the early years after restoration. Beside the influence of potential water pollution on the recovery of aquatic biota, the weaker or null trait responses of the aquatic biota may also be due to a degraded regional species pool limiting recolonization (Tonkin et al. 2014), degraded catchment or sub-catchment conditions (Lorenz & Feld 2013), or an inadequate degree of habitat change in the aquatic zone to trigger a biotic response (Hering et al. 2015). Indeed, restored channels often remain depleted of structures such as wood logs that are key drivers of aquatic habitat heterogeneity (Pilotto et al. 2016). Such in-channel structure would increase channel roughness and thus enhance channel retention capacity, increasing the retention of drifting plant propagules and animals (Engström et al. 2009). The lack of any increases neither in hydrochory for floodplain vegetation and macrophytes nor in passive aquatic dispersal for macroinvertebrates at restored reaches confirms that the restoration failed to reestablish complex in-channel structures. Moreover, hydrochory and macroinvertebrate drift, as well as fish dispersal (that was not addressed by restoration either), are strongly dependent on river longitudinal continuity, which is often neglected in reach-scale restoration projects and can only be addressed in a larger catchment-scale perspective. However, terrestrial groups are less dependent on longitudinal connectivity for dispersal than aquatic groups (Tonkin et al. 2016, 2018a). Carabid beetles, in particular, have a high overland dispersal ability (Desender 2000), which makes them fast colonizers of restored habitats (Lambeets et al. 2008).

Influences of Characteristics of the Restoration Projects, Rivers, and Data Sets on Restoration Outcomes

Communities undergo successional processes and recover from disturbance with time (e.g., Li et al. 2016). In our dataset with restorations spanning from 1 to 26 years old (mean = 8.4, SD = 5.3), however, the age of the restoration projects had no effect on the responses of any studied taxonomic groups. This result is in line with that of previous studies (Miller et al. 2010; Leps et al. 2016; Nilsson et al. 2017) and highlights that the recovery timeframe of good dispersers, such as carabid beetles, can

be short (Lorenz et al. 2018). The spatial extent of the restoration project resulted not critical in determining restoration outcomes, which confirms previous findings by Hering et al. (2015).

Catchment surface area was associated with increasing differences between control and restored reaches in terms of taxonomic richness and trait composition of fish and carabid beetles, and with decreasing differences in trait composition for macrophytes. The greater increase in taxonomic richness of fish in larger rivers can be explained by the generally higher richness from the rhithral to the potamal river zones (e.g., Oberdorff et al. 1993). Higher taxonomic richness subsequently provides a greater potential for trait differentiation in larger rivers. The greater increase in taxonomic richness and trait composition of carabid beetles at larger river reaches may reflect the potential higher availability of gravel and bars there, which are key habitats for this biotic group (Januschke & Verdonschot 2016). However, the opposite trend shown by macrophytes indicates a larger level of trait differentiation between restored and control reaches at smaller rivers. There, control impacted reaches were dominated (relative abundance ~60%) by helophytes, which are less dependent on river hydromorphological conditions than hydrophytes (Gantes & Caro 2001), whereas restored reaches and larger river reaches had a more differentiated macrophyte composition with higher shares of hydrophytes.

The different taxonomic groups included different numbers of taxa and were described by different numbers of trait modalities. These differences, however, did not influence our results, as the observed taxonomic and trait patterns did not reflect the patterns in number of taxa and trait modalities. For all studied groups, the level of taxonomic identification was species or genus, with the exception of benthic macroinvertebrates that were in some cases identified at family or subfamily level. Although this is the commonly used taxonomic level for such group in Germany (Haase et al. 2006), we cannot exclude that a better taxonomic resolution (e.g., for Chironomidae) could have revealed stronger biotic responses (e.g., Milošević et al. 2018).

Overall, our results indicate that hydromorphological restoration succeeded in increasing not only the physical but also the biotic diversity. This confirms the potential of hydromorphological restoration as a tool to stem or even reverse the current trends of increasing biotic homogenization and highlights its role for biological conservation. Hydromorphological restoration seems particularly effective for the conservation of highly specialized carabid beetles, which are currently partly endangered due to the strong anthropogenic pressures in most floodplains (Looy et al. 2005). Therefore, carabid beetles could be used to identify persisting deficits in riparian habitats (Januschke & Verdonschot 2016). The recovery patterns of each of the 5 taxonomic groups differed and revealed key independent insights on the recovery process. Specifically, terrestrial biota indicated a successful enhancement of lateral connectivity and the reestablishment of dynamic processes in the floodplain. In contrast, the rather weak response of aquatic biota to restoration suggests remaining issues in the aquatic ecosystem, such as degraded water quality. Therefore, a catchment scale approach to restoration should be encouraged to increase aquatic biodiversity. This could be achieved primarily by managing land use in the catchment (Feld 2013), restoring longitudinal connectivity and the connectivity with potential source populations (Stoll et al. 2013; Tonkin et al. 2014), and creating key habitats and hydromorphological complexity levels that are closer to undisturbed conditions (Hering et al. 2015; Pilotto et al. 2018).

The contrasting responses of aquatic and floodplain biota highlight the strong hydromorphological, functional, and biological interactions between the aquatic and floodplain ecosystems (Hjältén et al. 2016) and question the artificial separation of these 2 components of the riverine landscape by legislation. In Europe the Water Framework Directive (WFD) (2000/60/EC) focuses on the aquatic ecosystem, while floodplains are regulated by the Habitat Directive (92/43/EEC). Therefore, most river restoration projects are initiated by the WFD, whereas their effects seem more visible in the floodplain, assessments of which are run under the Habitat Directive. A more holistic approach that considers the effects of restoration on both components of the riverine landscape (e.g., analyzing different taxonomic groups) is needed to better preserve and enhance the whole river-floodplain system.

Acknowledgments

Supporting Information

Results of hydromorphological analyses (Appendix S1) and a description of sampling methods for the 5 studied taxonomic groups (Appendix S2) 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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