Hydrobiologia (2016) 769:55–66
DOI 10.1007/s10750-015-2575-8

RIVER RESTORATION EFFECTS

The role of benthic microhabitats in determining the effects of hydromorphological river restoration on macroinvertebrates

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Received: 3 February 2015 / Revised: 7 October 2015 / Accepted: 24 October 2015 / Published online: 20 November 2015

Abstract Despite the large number of river restoration projects carried out worldwide, evidence for strong and long-term positive ecological effects of hydromorphological restoration on macroinvertebrates is scarce. To improve the understanding of the success and failure of restoration measures, a standardized field study was carried out in nineteen paired restored and degraded river sections in mid-sized lowland and mountain rivers throughout Europe. We investigated if there were effects of restoration on macroinvertebrate biodiversity, and if these effects could be related to changes in microhabitat composition, diversity and patchiness. Effects were quantified for all taxa combined, as well as Ephemeroptera, Plecoptera and Trichoptera separately. Additionally, species trait classifications of microhabitat preference types were used as a functional indicator. Restoration had no overall positive effects on the selected macroinvertebrate metrics. Rather, we did find positive relationships between the macroinvertebrate responses and the effect of restoration on the diversity and patchiness of microhabitats. Furthermore, the effects on macroinvertebrates could be related to changes in the cover of specific substrate types in the restored sections. We conclude that the limited effect of restoration on macroinvertebrate diversity overall reflected, at least in part, the limited effect of most restoration measures on microhabitat composition and diversity.

Keywords Benthic invertebrates · River restoration · Microhabitat · Diversity · Richness

Guest editors: Jochem Kail, Brendan G. McKie, Piet F. M. Verdonschot & Daniel Hering / Effects of hydromorphological river restoration

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Introduction

A large number of river restoration projects have been carried out worldwide, aiming at restoring natural flow patterns and enhancing habitat heterogeneity to increase biodiversity, including that of macroinvertebrates. However, evidence for strong and long-term positive ecological effects of these measures on macroinvertebrates remains generally limited (e.g. Palmer et al., 2010; Feld et al., 2011; Friberg et al., 2014), despite some notable exceptions (Miller et al., 2010; Kail et al., 2015). These findings partly reflect the lack of robust scientific assessments of restoration measures, but even where such assessments have been carried out, changes in invertebrate diversity and community composition have often been minimal (e.g. Louhi et al., 2011; Ernst et al., 2012).

The low effectiveness of restoration on macroinvertebrates has been attributed to the limited scale of most restoration projects (Jähnig et al., 2010; Sundermann et al., 2011a), which have generally been small in comparison to total catchment size, often not exceeding a few kilometers of river length. If not removed or mitigated, environmental stressors acting at larger spatial scales, such as water quality, catchment land use and flow alterations often have an overriding influence on the recovery processes in these small restored sections (Feld et al., 2011; Verdonschot et al., 2013; Wahl et al., 2013). For example, local restoration measures aiming at restoring specific channel features that are undertaken without addressing larger-scale hydromorphological processes are often not sustainable, as seen when restoration of gravel beds is undermined by deposition of silt which clogs interstitial spaces, hindering the recovery of macroinvertebrate populations (Mueller et al., 2014). Finally, restoration effects can be expected to be minimal when source populations of targeted species are lacking within the catchment or migration barriers impede the colonization of the restored reaches (Lorenz & Feld, 2013; Kitto et al., 2015).

When looking at the reach scale, the effectiveness of generating greater habitat heterogeneity in restoration projects remains especially equivocal (Miller et al., 2010; Palmer et al., 2010; Roni et al., 2015). Although in most restoration projects, diversity of habitats, including microhabitats, increases considerably, this does not automatically result in a strong positive response by macroinvertebrate assemblages (Jähnig & Lorenz, 2008; Louhi et al., 2011). It is unclear to what extent this is the result of an overriding effect of catchment-scale hydromorphological, physicochemical or biological factors. Given the importance of microhabitats in structuring the macroinvertebrate assemblages in streams (e.g. Beisel et al., 1998), it might well be the case that the restoration measures applied simply do not result in restoring those key (micro)habitat elements or its spatiotemporal arrangement relevant to the targeted organisms in the course of their life cycle (Lepori et al., 2005; Lorenz et al., 2009).

We carried out a standardized field study in nineteen medium-sized lowland and mountain rivers across Europe (Muhar et al., this issue). In each river, we assessed the effectiveness of a restoration project with reference to a nearby non-restored, i.e. still degraded, section within the same river. First, we tested if restoration had an overall positive effect on total taxa richness and Shannon-Wiener diversity, as well as on the richness and diversity of Ephemeroptera, Plecoptera and Trichoptera (EPT), representing commonly used indicator groups which are sensitive to environmental stress (Lenat, 1984). To establish a more direct link to microhabitat changes resulting from restoration, macroinvertebrate microhabitat preference traits were included as a functional community measure (Feld & Hering, 2007; Mueller et al., 2014; Dolédec et al., 2015). Since the dataset comprised rivers which differed considerably from a typological point of view, in terms of restoration extent, and by restoration measures applied (Muhar et al., this issue), we also assessed how these factors affected the macroinvertebrate response to restoration. Second, we investigated if the effects of restoration on macroinvertebrates could be related to differences in the number, diversity and patchiness of microhabitats available in the restored and degraded river sections. Finally, if microhabitat composition appeared to be affecting the macroinvertebrate response to restoration, we tested which specific microhabitats were most important for the observed differences.

We expected that hydromorphological river restoration resulting in an increase in the number, diversity and/or patchiness of microhabitat types would have positive effects on both total and EPT richness and diversity. We expected even stronger responses for the metrics related to microhabitat/substrate preference of the assemblages, because these are more directly linked to changes in microhabitat composition. An increase in the number or diversity of microhabitats in the restored section should be reflected in the microhabitat preferences of the assemblage recorded, given that part of the stream macroinvertebrates can be regarded as microhabitat specialists (Schröder et al., 2013).

Methods

Study region and study design

Macroinvertebrate samples were taken in medium-sized lowland and mountain rivers across nine European countries: Finland, Sweden, Denmark, the Netherlands, Germany, Poland, the Czech Republic, Austria and Switzerland. Two rivers of comparable size and environmental characteristics were sampled per country, except for Germany where four streams were sampled from two regions: the lowlands and mountains. In each region, the two rivers comprised: (i) a river which contained a flagship restoration project, which represented a good-practice example of river restoration in the respective country (R1), and (ii) a river with a smaller restoration project (R2), which was shorter in restored river length, and/or where restoration was performed with lower "intensity" (fewer measures applied). The sampled section was always located in the downstream part of the restored reach. In both rivers, an additional non-restored, degraded section was sampled upstream of the restored section (respectively, D1 and D2) to serve as a control. The distance between the restored and non-restored section was chosen in such a way that it minimized the effects of differences in factors such as land use and discharge, but was large enough to prevent interference between both sections. In the German lowlands, only macroinvertebrate data from the river containing the flagship restoration site was available. As a consequence, in total nineteen rivers were sampled (ten R1 rivers and nine R2 rivers). A table providing detailed information about the environmental characteristics and restoration measures is given in Muhar et al., (this issue).

Sampling methodology

The sampling of benthic invertebrates followed EU Water Framework Directive (WFD) compliant sampling protocols (Haase et al., 2004). We performed the standardized multi-habitat sampling procedures developed in the AQEM and STAR projects, which reflects the proportion of the microhabitat types (substrate types according to Hering et al., 2003) that are present with >5% cover. Samples were taken from a 200-m-long river section during June to July. In each section sampled, 20 individual benthic invertebrate samples (sample units) were taken with a hand-net/shovel sampler or a Surber-sampler with a mesh size of 500 μm. The sampled area was 25 × 25 cm each, resulting in 1.25 m^2 of river bottom being sampled. A 'sampling unit' consisted of an area upstream of the net equivalent to the square of the net frame (0.25 × 0.25 m). The 20 sampling units were distributed according to the share of microhabitats. For example, if 50% of the sampling reach was covered with sand, half of the sampling units (10 out of 20) were taken on sand.

In the field, the 20 samples obtained from each sampling reach were pooled and preserved with ethanol (96%). In the laboratory, subsampling was used to reduce the effort required for sorting and identification while also providing an unbiased representation of the total sample (Caton, 1991; Haase et al., 2004). Specifically, a minimum amount of 1/6th of the material was subsampled, containing a minimum number of 350 individuals. The subsampled individuals were sorted according to Haase et al., (2004) and identified to the lowest possible level as suggested by Haase et al., (2006), generally species or genus, but to a higher level in Diptera (mostly to family), Oligochaeta (class) and Hydrachnidia (subcohort).

Biological metrics

As not all macroinvertebrate specimens collected were identified to the same taxonomic level, an adjustment procedure was applied (e.g. Vlek et al., 2004) to reduce bias in the subsequent analyses by grouping to a higher taxonomical level (Schmidt-Kloiber & Nijboer, 2004). The total number of macroinvertebrate taxa and Shannon–Wiener diversity (Shannon & Weaver, 1949), as well as the total number of Ephemeroptera, Plecoptera and Trichoptera taxa (EPT) was calculated for each river section. Species trait classifications characterising macroinvertebrate microhabitat/substrate preferences were derived from the freshwaterecology.info database (Schmidt-Kloiber & Hering, 2015), but only for Ephemeroptera, Plecoptera and Trichoptera, for which these preferences were consistently available). The number of microhabitat types (e.g. pelal, psammal and macrophytes) covered by the assemblage in each river section was quantified to get an indication of the number of potentially occupied microhabitats present in the river section. Additionally, the Shannon–Wiener diversity (Shannon & Weaver, 1949) index of microhabitat preferences was calculated according to the following formula:

$$H' = -\sum_{i=1}^{S}(p_i)(\log p_i),$$

where H' is the index of microhabitat/substrate preference type diversity, S the number of microhabitat preferences covered by the macroinvertebrate assemblage in a river section, and p_i the proportion of the total preference scores of a river section (sum of all points assigned to the taxa across microhabitat types) belonging to the ith microhabitat type. A low microhabitat/substrate preference diversity indicates that the river section is occupied by an assemblage with relatively homogenous microhabitat/substrate preferences, which might reflect a low diversity of microhabitats in the system.

Microhabitat composition

In each 200-m-long river section, microhabitat composition was recorded along ten transects. Along each transect dominant, substrates (substrate types according to Hering et al., 2003) were recorded visually at ten equidistant survey points. The mean number and Shannon–Wiener diversity (Shannon & Weaver, 1949) of natural substrates was calculated for each transect. Artificial substrates like riprap or concrete walls were excluded because they were generally removed during restoration. Furthermore, the spatial arrangement of microhabitats was included by calculating the spatial diversity index (SDI; Fortin et al., 1999; Jähnig et al., 2008; Sundermann et al., 2011a). The SDI acts as an index of microhabitat patchiness, in considering both the spatial arrangement as well as the number and area of substrate patches along the transects and was calculated according to the following formula:

$$\mathrm{SDI} = \sum_{i=1}^{S}\frac{\text{number of patches of substrate i}}{\text{range of area occupied by substrate i}},$$

where S is the number of substrates in a transect.

Data analysis

We first assessed whether there was an overall positive effect of restoration on the absolute values of the selected richness and diversity metrics by a group- and pairwise comparison of all restored (R) and degraded (D) river sections using Mann–Whitney U tests and Wilcoxon-Matched Pairs tests. Second, to quantify the effects of restoration on the selected macroinvertebrate metrics, effect sizes were calculated. We used (i) the pairwise calculation of the difference between each pair of restored and degraded section, and (ii) a modified version of the Osenberg et al. (1997) response ratio Δr_{m} (the modification was necessary to correct for 0-values in the dataset), according to the following formula:

$$\Delta r_{\mathrm{m}} = \ln\left(\frac{(1+X_{\mathrm{R}})}{(1+X_{\mathrm{D}})}\right),$$

where X_{R} is the richness or diversity of the restored section and X_{D} of the degraded section. Values >0 denote a positive effect (e.g. increase of richness or diversity), and negative values denote a negative effect. Using the response ratio enabled us to directly compare the effect of restoration on different metrics, using t tests to assess whether the mean effect sizes differed significantly from zero (with zero indicating no effect). Differences in response between the two main river types studied (gravel-cobble bed mountain rivers and sand-bed lowland rivers), restoration extent (flagship sites: R1, and normal sites: R2) and the main restoration measures applied (widening, re-meandering and re-connection, instream measures) were tested using Mann–Whitney U tests and Kruskal–Wallis tests.

Third, relationships between differences in microhabitat composition between the paired restored and degraded river sections and the responses of the selected macroinvertebrate metrics were investigated. Spearman rank order correlations were used to investigate bivariate relationships between the response ratios of the microhabitat variables recorded in the river sections and the selected macroinvertebrate metrics. Effect ratios for the microhabitat variables were based on the mean of the ten transects per river section. Only the common microhabitats ($n > 5$ rivers) in the dataset were analysed. Significance testing was carried out in IBM SPSS for Windows (version 19).

Results

Overall effects of restoration on macroinvertebrates

Neither an overall comparison of the restored and degraded sections (Mann–Whitney U tests, $P > 0.05$,

$n = 38$; Fig. 1), nor pairwise comparisons of the restored and corresponding degraded sections (Wilcoxon-Matched Pairs tests, $P > 0.05$, $n = 19$) revealed significant differences between restored and degraded river sections for the selected macroinvertebrate richness and diversity metrics. Moreover, pairwise calculated effect sizes, whether expressed as the absolute difference between the restored and degraded sections (Fig. 2), or as the relative difference (modified Osenberg response ratios; Fig. 3) showed no significant effect of restoration, i.e. mean values were not significantly different from zero (t tests, $P > 0.05$, $n = 19$). However, variability was high, especially for macroinvertebrate richness, reflecting widely contrasting responses between different projects, with the number of taxa sometimes increasing and other times decreasing substantially after restoration (Figs. 2A, 3).

There were no significant differences in neither the absolute effect sizes nor for the response ratios, between according to river type (sand $n = 7$, gravel-cobble $n = 12$), rivers restoration extent (R1 $n = 10$, R2 $n = 9$), or restoration measures applied (widening $n = 8$, instream measures $n = 5$, re-meandering and re-connection $n = 6$) (Mann–Whitney U tests and Kruskal–Wallis tests, $P > 0.05$). Similarly, a paired comparison of the restoration extent per country (the R1 river section compared to the corresponding R2 river section) did not reveal any significant differences (Wilcoxon-Matched Pairs tests, $P > 0.05$, $n = 9$).

Relationships between macroinvertebrates and microhabitat composition, diversity and patchiness

The effects of restoration on total richness and the diversity of EPT taxa were significantly related to the difference in microhabitat diversity between the restored and degraded river sections: an increase in microhabitat diversity generally coincided with higher response ratios for total richness and diversity of EPT taxa (Spearman rank correlations, $P < 0.05$, $n = 19$; Table 1; Fig. 4A, B). Furthermore, the effect of restoration on microhabitat patchiness was significantly related to the effect on EPT taxa richness and microhabitat preference types diversity (Spearman rank correlations, $P < 0.05$, $n = 19$; Table 1; Fig. 4C, D): response ratios were generally higher in river sections with an increased spatial diversity index value, e.g. rivers where in the restored sections more, and more evenly distributed, microhabitat patches were available.

Differences in cover in several of the microhabitat types (mesolithal, psammal, coarse and fine particulate organic matter) recorded in the restored and degraded river sections were significantly related to differences in several of the macroinvertebrate metrics (EPT and microhabitat preference types richness and diversity) (Spearman rank correlations, $P < 0.05$; Table 2). An increase in the cover of cobbles (mesolithal) was related to a higher EPT richness

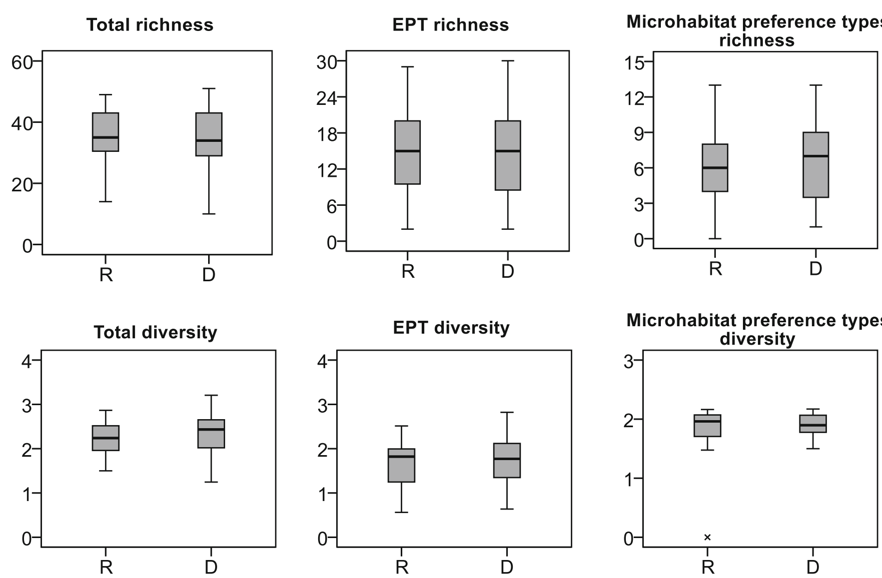

Fig. 1 Comparison of the richness and diversity metrics between restored (R) and degraded sections (D), pooled across study reaches. Plots show median, box: 25–75%, whisker: non-outlier range, and x = extreme value

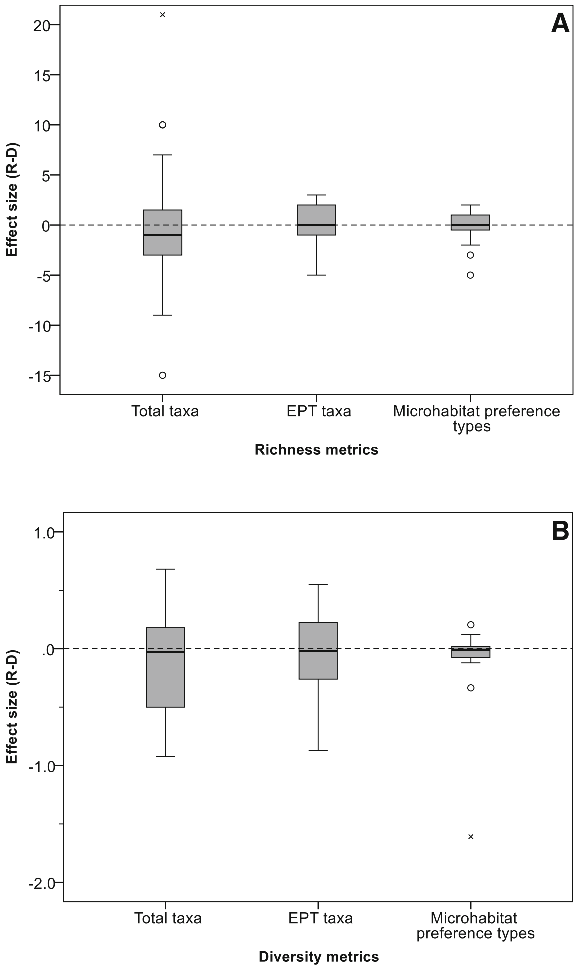

Fig. 2 Effects of restoration on richness (**A**) and diversity (**B**) metrics using the absolute effect size: Restored (R)—Degraded (D). Plots show median, box: 25–75%, whisker: non-outlier range, ○ = outliers, and × = extreme values

and a higher number of microhabitat preference types (Fig. 5A, D). Moreover, an increase in sand cover (psammal) and coarse particulate organic matter cover were related to an increase in EPT diversity (Fig. 5B, C). Finally, a decrease in the cover of fine particulate organic matter was related to an increase in microhabitat preference types diversity (Fig. 5E).

Discussion

No overall effects of restoration on any of the selected macroinvertebrate metrics were detected based on our comparisons of restored and upstream degraded river sections throughout Europe. These results are consistent with other restoration studies, which indicated that hydromorphological restoration measures increasing structural heterogeneity or restoring natural flow regimes did not generally promote macroinvertebrate biodiversity, even if habitat changes were considerable (Lepori et al., 2005; Jähnig et al., 2010; Palmer et al., 2010; Haase et al., 2013; Friberg et al., 2014). Nonetheless, by employing an alternative approach based on quantification of microhabitat diversity and patchiness rather than restoration *per se*, we were able to identify some important cases where restoration did have positive effects on macroinvertebrate metrics. Specifically, we identified cases where restoration was linked with both increased patchiness of microhabitats, and macroinvertebrate diversity, and we also detected relationships between changes in specific substrate types and macroinvertebrate diversity following restoration.

The correlations we detected between the selected macroinvertebrate metrics and microhabitat composition, diversity and patchiness indicate that reach-scale restoration can add to an increase in macroinvertebrate richness and diversity if the ecologically relevant habitats are restored. Limited availability of key microhabitats in restored rivers might hinder colonization by additional species (Lorenz et al., 2009). Restoring these microhabitats, such as stones covered by aquatic mosses and large woody debris, might render relatively large effects because they can be regarded as key habitat elements for a relatively large number of (specialized) species (McKie & Cranston, 1998, 2001; Feld & Hering, 2007; Miller et al., 2010; Louhi et al., 2011). Here also a disparity in the effects of microhabitat types was found; of all microhabitat types investigated, positive effects on EPT richness or diversity were found for cobbles, sand and especially coarse particulate organic matter. In line with our results, Jähnig & Lorenz (2008) showed that cobbles and coarse particulate organic matter in restored rivers were particularly rich in macroinvertebrates. It is likely that these structural complex microhabitats add to a positive response to restoration by providing resources in the form of food, shelter and attachment sites (Downes et al., 1998). Although richness and abundance of sand is generally lower in comparison to less dynamic substrates, it harbors a distinct community of macroinvertebrates (Yamamuro & Lamberti, 2007), which might explain the positive relationship

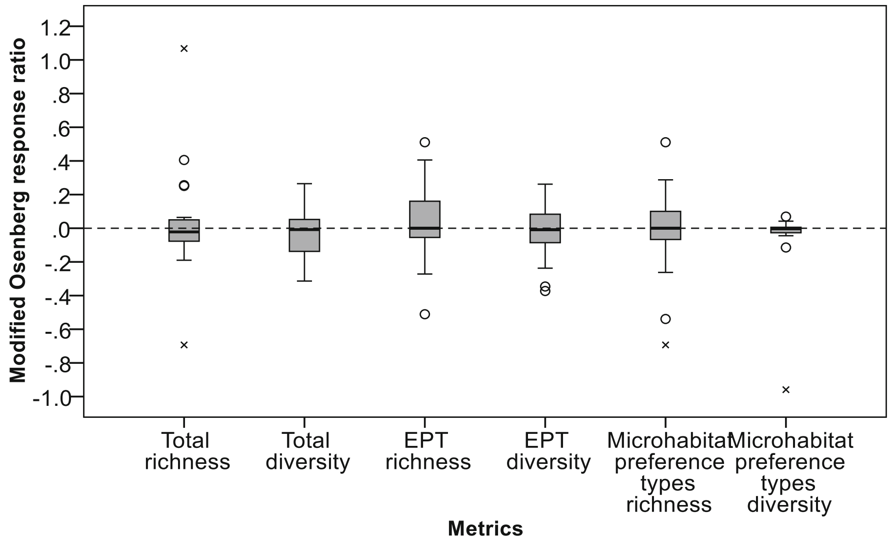

Fig. 3 Effects of restoration on richness and diversity metrics using the modified Osenberg response ratio (Δr_m). Plots show median, box: 25–75%, whisker: non-outlier range, ○ = outliers, and × = extreme values

Table 1 Correlation matrix (Spearman rank order) of the modified Osenberg response ratios (Δr_m) of the selected macroinvertebrate metrics and the Osenberg response ratios (Δr) for three variables describing the difference in microhabitat composition between the restored and degraded river sections ($n = 19$): number of microhabitats (#), microhabitat diversity (Shannon–Wiener index; SWI), and microhabitat patchiness (spatial diversity index; SDI)

Metric	Spearman rank order (ρ) of modified response ratios		
	#	SWI	SDI
Total richness	0.32	0.47*	0.20
Total diversity	0.21	0.20	0.23
EPT richness	0.27	0.30	0.47*
EPT diversity	0.39	0.58**	0.18
Microhabitat preference types richness	0.13	−0.01	0.39
Microhabitat preference types diversity	0.39	0.31	0.69**

Significance * $P < 0.05$, ** $P < 0.01$

with EPT diversity we observed in rivers were sand cover increased after restoration.

Conversely, our findings also indicate that the general lack of an effect of restoration on microhabitat composition and diversity in many of our studied rivers could be a key factor explaining the lack of response in the overall comparisons of the selected macroinvertebrate metrics. Microhabitat composition and diversity are not explicitly manipulated in many restoration projects, but rather are expected to improve as a consequence of restoring meso- or macrohabitat conditions (e.g. restoration of sinuosity is expected to rehabilitate microhabitats in stream bends). In other words, while restoration projects involving measures such as widening and re-meandering are visually appealing and generally increase habitat diversity, this does not automatically result in sufficient restoration of all microhabitats relevant for the targeted macroinvertebrate community, for example, in terms of microhabitat type, proportional cover and spatial arrangement (Jähnig & Lorenz, 2008; Lorenz et al., 2009).

Not only the mere presence, cover or spatial arrangement of microhabitats, but also the environmental quality of the restored habitats, and of the reaches more generally, could be important in explaining the general lack of response by macroinvertebrate assemblages following restoration. Since species often have specific microhabitat requirements throughout their life, all these habitats must be present

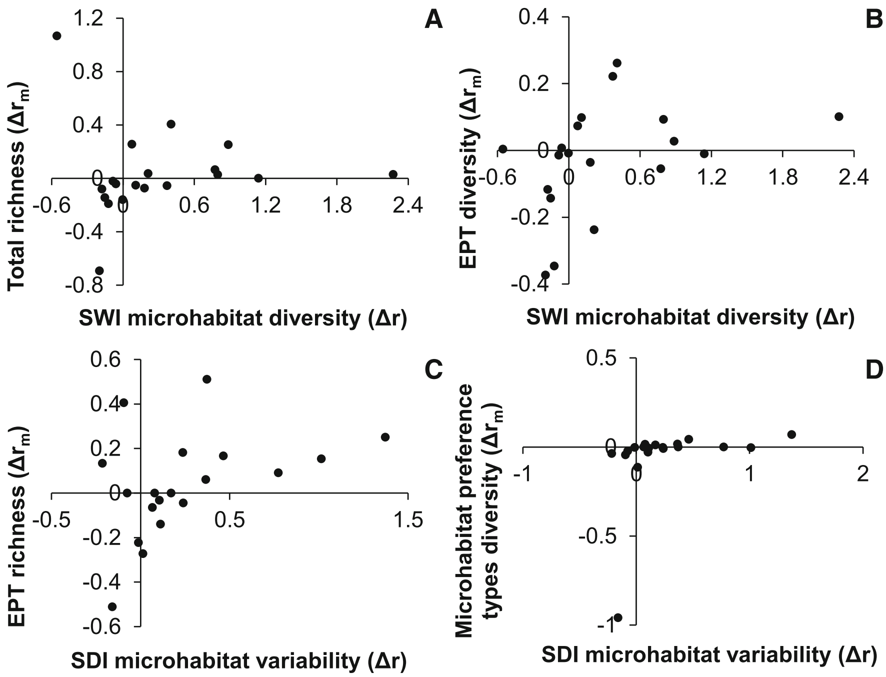

Fig. 4 Relationships between the differences in microhabitat diversity and patchiness between the restored and the degraded river sections, expressed as the Osenberg response ratio (Δr) of the microhabitat diversity (Shannon–Wiener Index; SWI) and de microhabitat patchiness (Spatial Diversity Index; SDI), and its associated differences in macroinvertebrate metrics, the modified Osenberg response ratio (Δr_m) for: **A** total richness, **B** EPT diversity, **C** EPT richness, and **D** Microhabitat preference types diversity. Values > 0 denote a positive effect, and negative values denote a negative effect

and of sufficient quality to guarantee recolonization and the development of sustainable populations. Unfortunately, assessing the quality of the microhabitats was not part of our study, which makes it difficult to estimate its importance. More generally, the impact of landscape-level stressors not mitigated by the restoration measures applied, such as eutrophication, a high organic load, pesticides, siltation, large water temperature fluctuations, and low and high flows, might simply have constrained the effect of local-scale restoration measures (e.g. Sarriquet et al., 2007; Palmer et al., 2010; Feld et al., 2011; Haase et al., 2013). To complicate the habitat-species relationship further, both local and landscape-scale stressors can also affect specific habitat needs of the terrestrial life stages of aquatic insects by impacting the riparian zone. The habitat quality of the riparian zone may have a large impact on the survival and reproduction success of the adult life stages through, amongst others microclimate, habitat structure, plant species composition and food availability (Hoffmann, 2000; Harrison & Harris, 2002; Briers & Gee, 2004). In this study, only the aquatic microhabitat conditions are evaluated in detail, whilst the terrestrial habitat is treated on a different and a less detailed scale, for example, as adjacent land use categories. Therefore, it is well possible that factors potentially structuring the macroinvertebrate assemblage have been overlooked.

We found no differences in restoration effects on the selected macroinvertebrate metrics between flagship and normal restoration projects and detected no differences when the effects of the different restoration measures were compared. These results might point towards the above-mentioned landscape-scale environmental stressors causing the observed lack of response, overruling the local-scale effects of restoration extent. On the other hand, the underlying cause could also be biological and historical; a depleted regional species pool might have constrained the effect of restoration (Sundermann et al., 2011b; Haase et al., 2013). Even if the restored river sections were suitable for the targeted macroinvertebrates based on their environmental conditions, recolonization will be unlikely on the short term when the distance between a

Table 2 Correlation matrix (Spearman rank order) of the modified Osenberg response ratios (Δr_m) of the selected macroinvertebrate metrics and the Osenberg response ratios (Δr) describing the differences between the restored and degraded river sections for the major microhabitats recorded

Microhabitat	Spearman rank order (ρ)						n
	Total richness	Total diversity	EPT richness	EPT diversity	Microhabitat preference types richness	Microhabitat preference types diversity	
Macrolithal (blocks)	0.37	−0.11	−0.36	0.04	−0.15	0.02	12
Mesolithal (cobbles)	0.34	0.22	0.491	0.09	0.59*	0.47	17
Microlithal (coarse gravel)	0.00	0.31	0.05	0.36	−0.26	0.35	16
Akal (fine gravel)	−0.07	0.05	0.34	−0.14	0.27	0.40	9
Psammal (sand)	0.14	0.01	0.08	0.46*	−0.07	0.14	19
Argyllal (loam, clay)	0.06	0.06	0.17	0.00	0.27	0.28	14
Coarse particulate organic matter	0.58	−0.07	−0.25	0.85**	−0.50	−0.54	10
Fine particulate organic matter	0.09	0.31	−0.33	0.23	−0.37	−0.65*	12
Living parts of terrestrial plants	−0.34	−0.63	0.02	−0.45	0.08	−0.41	7
Submerged macrophytes	−0.55	−0.16	0.11	−0.33	−0.17	−0.06	7

Significance * $P < 0.05$, ** $P < 0.01$

restored river section and a potential source population is large and the targeted species have a low dispersal ability (Tonkin et al., 2014). In our study, the mean project age for the rivers studied was ten years, which might be sufficient for more strongly dispersing taxa to reach the restored site (Fuchs & Statzner, 1990), but perhaps not for weaker dispersers (e.g. those lacking an adult flying stage, or with short-lived weak-flying adults) hindered by barriers either within river networks (e.g. dams) or in the terrestrial landscape (e.g. exposed conditions in agricultural or urban landscapes).

We used the number of microhabitat preference types and its diversity as functional metrics of microhabitat composition, because we expected that this gave a more direct link with the habitat use of the macroinvertebrates recorded. Both the richness and Shannon diversity of microhabitat preference types displayed relationships with the microhabitat variables analysed. Several of the functional trait relationships found were not detected using the taxonomical metrics. This indicated an additional value of using functional measures besides the traditional taxonomical ones, as also highlighted by Feld & Hering (2007). Microhabitat preference types diversity increased when more microhabitats with a more evenly distribution were available in the restored river sections. Furthermore, relationships were detected between the richness of microhabitat preference types, and an increase in the proportional cover of cobbles after restoration and a decrease of the cover of fine particulate organic matter. This suggests that restoration involving an increase in cobble microhabitat coincides with the generation of other microhabitats preferred by macroinvertebrates, which is likely the consequence of the heterogeneous nature of cobble riverbeds as well as their relative stability (Beisel et al., 1998). The negative effect of an increase of the proportional cover of fine particulate organic matter on the microhabitat preference types diversity could be explained by the loss of specific microhabitats due to deposition of fines in low flow areas (Jones et al., 2012).

Given the equivocal effects reported in studies on the macroinvertebrate responses to hydromorphological restoration, it is very important to further clarify the relative contribution of local-scale factors (the role of microhabitats, both aquatic and riparian) versus landscape-scale factors (environmental stressors, lack of colonists) to successful restoration. This is especially so given that addressing factors operating at different spatial scales will require different restoration approaches. The results of the present study show that many restoration projects might have had a low effect on macroinvertebrate communities due to a low effect of the restoration measures on microhabitat diversity,

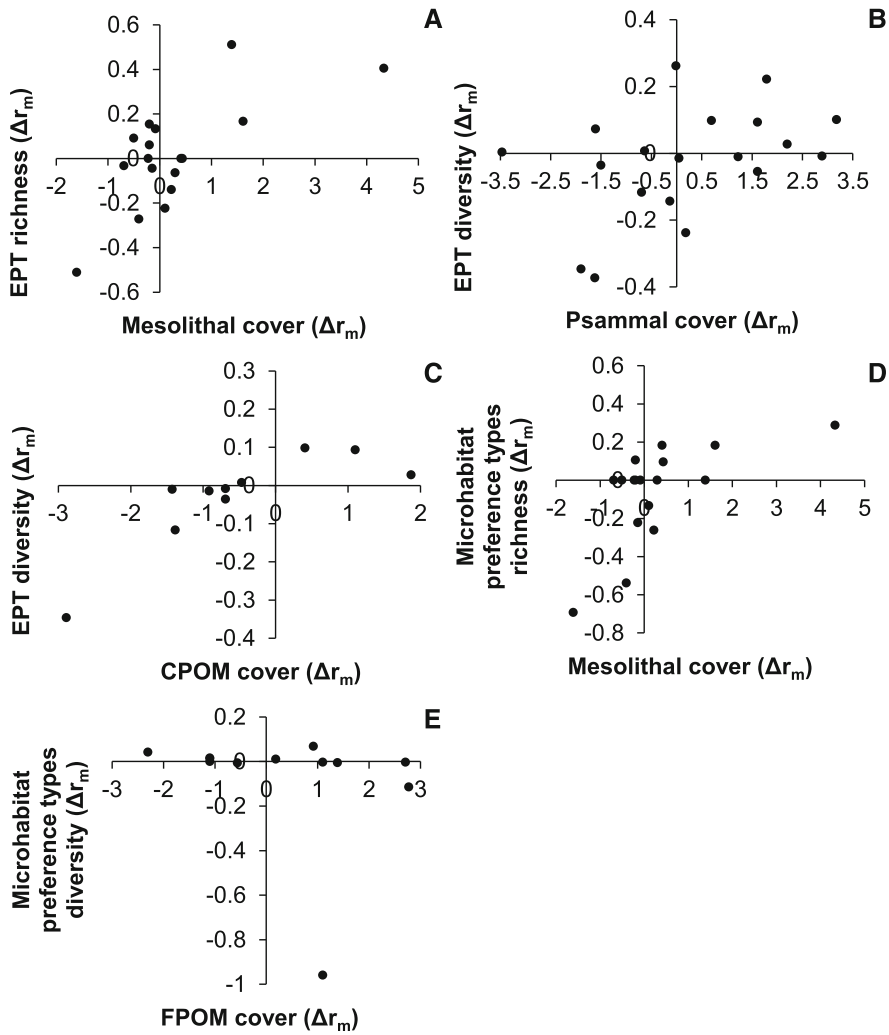

Fig. 5 Relationships between the differences in the cover of microhabitat types **A**, **D** mesolithal (cobbles), **B** psammal (sand), **C** coarse particulate organic matter (CPOM), and **E** fine particulate organic matter (FPOM) between the restored and the degraded river sections and its associated differences in macroinvertebrate richness and diversity metrics, expressed as modified Osenberg response ratios (Δr_m). Values >0 denote a positive effect, and negative values denote a negative effect

highlighting the importance of restoring physical habitat conditions which are ecologically relevant. For future restoration projects to be successful in terms of macroinvertebrate biodiversity, we recommend a more integrated approach which involves simultaneously tackling problems on different spatial scales, from enhancing the habitat quality on microhabitat scale to removing or mitigating stressors impacting whole drainage basins, but always with the ecological habitat requirements and/or life history of the targeted macroinvertebrate species in mind.

Acknowledgments We thank Armin Lorenz and two anonymous reviewers for their helpful comments on an earlier version of this manuscript. The study was supported by the EU-funded Integrated Project REFORM (Restoring rivers FOR effective catchment Management; European Union's Seventh Programme for research, technological development and demonstration under Grant Agreement No. 282656).

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