Scale-dependent effects of river habitat quality on benthic invertebrate communities — Implications for stream restoration practice

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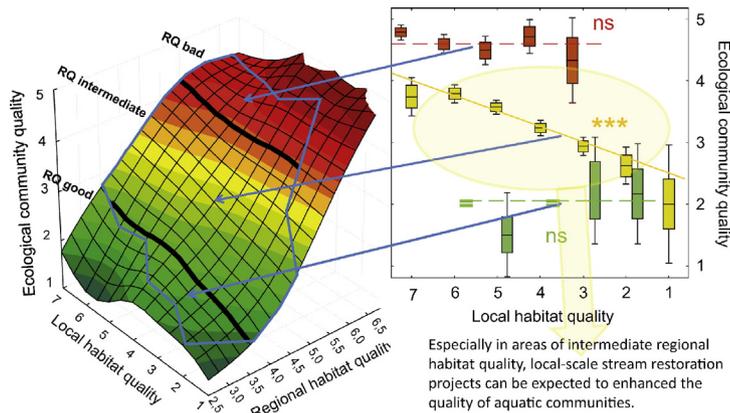[c] Oregon State University, Department of Integrative Biology, 3029 Cordley Hall, 2701 SW Campus Way, Corvallis, OR 97331, USA
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HIGHLIGHTS

- Local- and regional scale habitat quality exert interactive effects on stream communities.
- At high or low regional habitat quality, community quality was independent of local habitat quality.
- Only in areas of intermediate regional habitat quality did communities respond to local habitat quality.
- Metacommunity structure and processes are analyzed to explain these results.
- Spatial prioritization strategies for stream restoration projects are derived.

GRAPHICAL ABSTRACT

Especially in areas of intermediate regional habitat quality, local-scale stream restoration projects can be expected to enhanced the quality of aquatic communities.

ARTICLE INFO

ABSTRACT

Although most stream restoration projects succeed in improving hydromorphological habitat quality, the ecological quality of the stream communities often remains unaffected. We hypothesize that this is because stream communities are largely determined by environmental properties at a larger-than-local spatial scale. Using benthic invertebrate community data as well as hydromorphological habitat quality data from 1087 stream sites, we investigated the role of local- (i.e. 100 m reach) and regional-scale (i.e. 5 km ring centered on each reach) stream hydromorphological habitat quality (LQ and RQ, respectively) on benthic invertebrate communities. The analyses showed that RQ had a greater individual effect on communities than LQ, but the effects of RQ and LQ interacted. Where RQ was either good or poor, communities were exclusively determined by RQ. Only in areas of intermediate RQ, LQ determined communities. Metacommunity analysis helped to explain these findings. Species pools in poor RQ areas were most depauperated, resulting in insufficient propagule pressure for species establishment even at high LQ (e.g. restored) sites. Conversely, higher alpha diversity and an indication of lower beta dispersion signals at mass effects occurring in high RQ areas. That is, abundant neighboring populations may help to maintain populations even at sites with low LQ. The strongest segregation in species co-occurrence was detected at intermediate RQ levels, suggesting that communities are structured to the highest degree by a habitat/environmental gradient. From these results, we conclude that when restoring riverine

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habitats at the reach scale, restoration projects situated in intermediate RQ settings will likely be the most successful in enhancing the naturalness of local communities. With a careful choice of sites for reach-scale restoration in settings of intermediate RQ and a strategy that aims to expand areas of high RQ, the success of reach-scale restoration in promoting the ecological quality of communities can be greatly improved.

1. Introduction

Streams and rivers are among the most threatened ecosystems of the world (Naiman and Turner, 2000; Dudgeon et al., 2006). The origin of this threat is excessive anthropogenic use, which has caused a physicochemical and hydromorphological degradation of many riverine ecosystems. Stimulated by the EU Water Framework Directive (WFD) (European Commission, 2000) and similar legislation worldwide, stream restoration projects are being conducted in many countries to improve habitat quality (Bernhardt et al., 2005; Palmer et al., 2005; Dudgeon et al., 2006). These restoration projects are still most often based on the assumption that if the hydromorphological quality of the stream is restored, the biological diversity will also be benefit (Palmer et al., 1997; Kail and Hering, 2009). This restoration approach follows the "Field of Dreams Hypothesis" (Palmer et al., 1997) assuming that "if you build it, they will come".

However, although the correlation between local habitat quality and biodiversity has been claimed (Frissell et al., 1986) and supported in principle by many studies (e.g. Völker and Borchardt, 2007; Kovalenko et al., 2012), many stream restoration projects at the reach scale have not yet shown the expected outcomes; even where habitat quality was significantly improved, a positive effect on benthic invertebrate as well as fish communities often did not materialise (Pretty et al., 2003; Lepori et al., 2005; Roni et al., 2008; Palmer et al., 2010; Vehanen et al., 2010; Louhi et al., 2011; Dolédec et al., 2015; Thomas et al., 2015; but see also: Miller et al., 2010; Lorenz et al., 2013). Several reasons for this lack in community response to reach-scale restorations have been discussed, including the hypotheses that (i) some sampling designs might be inadequate to detect restoration effects (Vaudor et al., 2015), (ii) communities are affected by multiple stressors, and remaining stressors not addressed by the restoration limit community recovery (Palmer et al., 2010; Leps et al., 2015), (iii) restorations suffer from a mismatch in the spatial scales of the environmental stressor and restoration projects (Bond and Lake, 2003; Lake et al., 2007; Roni et al., 2008; Feld et al., 2011) and (iv) the recolonisation potential from surrounding stream reaches is low because of large-scale depauperation of species pools (Sundermann et al., 2011; Stoll et al., 2013, 2014; Tonkin et al., 2014). Hypotheses (iii) and (iv) reflect the principle that local communities are always part of a metacommunity that is maintained through dispersal and operates primarily at the regional scale (Bohonak and Jenkins, 2003; Leibold et al., 2004; Brown et al., 2011).

Despite the knowledge that communities are also determined by regional-scale processes and structures (Poff, 1997; Lake et al., 2007), the role of regional- vs. local-scale habitat variables has rarely been tested with empirical data in a restoration context. In this study, we therefore analyze the interplay of local and regional stream habitat quality in determining local communities, using benthic invertebrates as a test case. Similar to Poff's filter model (Poff, 1997), we expect hierarchical effects of regional and local habitats, with regional habitat as the overriding community structuring agent, and local habitat playing a secondary role. In terms of metacommunities within these areas, we expected more diverse regional species pool where regional habitat quality was higher. Given a high connectedness in such high quality areas, this is expected to lead to a swamping of local niche control by local habitat quality through species spilling over into poor local habitats (i.e. mass effects). In poor regional habitat conditions, in turn, even high quality local habitats are not adequately colonized due to the lack of dispersing organisms that could found and sustain local populations (Sundermann

et al., 2011). In restoration planning, it is still often assumed that dispersal is virtually unlimited, leading to rapid colonization of any new habitat. Furthermore, based on a recent study that found anthropogenic habitat modification disrupted co-occurrence patterns in stream invertebrate communities (Larsen and Ormerod, 2014), we expected an increasing randomization of co-occurrence patterns from good to poor regional habitat quality sites.

To test these assumptions, we examined components of the metacommunity structure of each region, including richness, beta diversity, and co-occurrence patterns. These analyses can help to disentangle local and regional effects and identify potential causal mechanisms that shape local community patterns.

Specifically, the following hypotheses were tested: (1) local communities are largely determined by regional-scale stream habitat quality, while local-scale stream habitat quality plays a subordinate role; (2) local- and regional-scale habitat quality do not affect local invertebrate communities independently, but interactively; (3) this results from an interplay between species depauperation of regional species pools with poor regional habitat quality at one end of the scale (i.e. dispersal limitation) and mass effects swamping niche control in regions with high regional habitat quality at the other end of the regional habitat quality scale.

Knowledge of the effects of habitat quality at different spatial scales as well as their interactions in determining communities will be helpful to conceptualize efficient and successful reach-scale stream restoration. Thus, our results can help to establish criteria for spatial prioritization of potential restoration sites, to define configurations for multiple reach-scale restoration designs, and to forecast potential restoration outcomes to avoid costly failures of restoration projects that do not meet their anticipated targets.

2. Materials and methods

2.1. Benthic invertebrate assessment

We analyzed benthic invertebrate community data from 1087 sampling sites in Hesse, Central Germany (Fig. 1). Samples were taken between 2005 and 2008 using the EU WFD compliant German standard multi-habitat sampling method (Haase et al., 2004). Each sample represented the local invertebrate community on a 50–100 m long stream reach. Species were identified according to the minimum requirements of the official taxa list according to the WFD (Haase et al., 2006), i.e., mostly at the species or the genus level. To minimize potential biases in metacommunity structure that might be induced by differences in connectivity along the dendritic stream networks (Brown and Swan, 2010; Brown et al., 2011), as well as other influences in broad-scale physical conditions, we limited the stream types included in the analysis. We selected sites in small and medium size streams in lower mountain areas (stream types 5, 5.1 and 9 according to Sommerhäuser and Pottgiesser, 2008) of the European Central highlands ecoregion (European Commission, 2000), which are at the same time the most common stream types in the study region. For each benthic invertebrate community sample, we calculated the ecological quality class (EQC) using the ASTERICS program (ASTERICS, 2011). EQC is an abundance-weighted summary metric addressing the susceptibility of local species to different types of degradation. As EQC is the relevant metric to monitor benthic invertebrate community quality in the EU WFD it is commonly used by water managers in the European Union. It is also commonly used to assess stream restoration outcomes (Kail and Hering, 2009; Gellert et al., 2012;
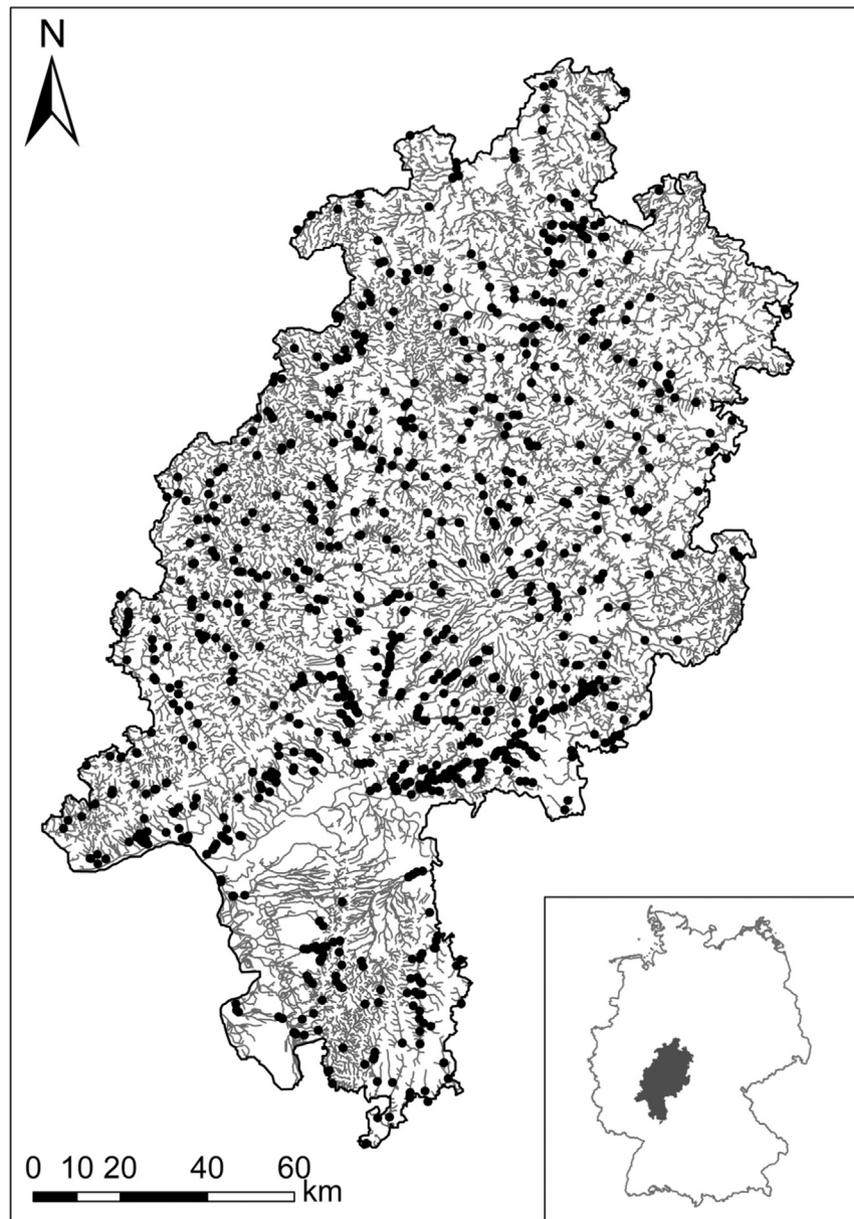
Fig. 1. Map of the benthic invertebrate sampling sites located in streams in Hesse, Germany.

Kail et al., 2012). EQC values range from 1 (high community quality) to 5 (bad community quality).

2.2. Stream habitat quality

Hydromorphological stream habitat quality was assessed based on the German standard habitat survey scheme (LAWA, 2000). The Hessian Agency for the Environment and Geology provided the latest state-wide assessment as a geodatabase, containing all streams in the entire Hessian stream network, divided into contiguous 100-m sections. The hydromorphological habitat quality data comprised the six main parameters of this stream habitat survey (plan form, longitudinal profile, bed structure, cross-section, bank structure, floodplain corridor), each ranging from 1 (undisturbed) to 7 (totally disturbed) (Kamp et al., 2007). The total local hydromorphological stream habitat quality (LQ) was calculated from these six main parameters for each 100 m stream reach (for details about the hydromorphological stream habitat quality assessment see also Appendix A). In Hesse, LQ values ranged between 1.2 and 7.0. The most common elements of stream habitat degradation were, first, river training leading to monotonous cross profiles with strongly reduced variability of stream width and water depth in 43% of all stream reaches, and second, poor status of the adjacent floodplain habitats, mostly due to intense agricultural use in 40% of all reaches. Flow diversity and as a consequence, substrate mobility with erosion-sedimentation dynamics was heavily or totally disturbed in 30% of the reaches. Finally, stream beds were degraded, i.e. scoured, silted or completely artificial, in 25% and riparian zones were impacted by artificial embankment structures in 21% of the reaches. Hesse is densely populated (approx. 6.1 Mio inhabitants on 21,000 km^2 of land in 2014). About 40% of the land is used by agriculture and another 40% is covered by forest. Larger, intact forest fragments with high RQ streams, however, occur predominantly in lower mountain areas, e.g. in the Vogelsberg, the Kellerwald and the Rothaargebirge.

As a measure of regional hydromorphological stream habitat quality (RQ), we averaged the LQ values of all individual 100 m reaches within a radius of 5 km around each sampling site. This approach was chosen based on the findings of Sundermann et al. (2011), showing that the regional species pool from which restored reaches are recolonized is

largely limited to this distance. Analogous to their approach we also defined the regional surroundings by a fixed radius, not by along-stream distances. This definition is appropriate because many species of benthic invertebrates have winged stages and also fly across land. Thus, even stream reaches that may have a longer along-stream distance than 5 km to a given site may influence local communities through terrestrial/aerial dispersal (Hughes, 2007; Geismar et al., 2015). LQ and RQ can theoretically be considered as independent measures of habitat quality at their respective spatial scale, as each RQ value is the average of >100 LQ values, and only one of them representing the site at which the macroinvertebrate sample has been taken. However, as neighboring reaches tend to have similar LQs, a moderate, but uncritical correlation between LQ and RQ emerges (r = 0.46; VIF = 1.27).

As considerable proportions of Hesse are used for agriculture, besides habitat degradation, chemical water quality and water temperature can be an issue for aquatic communities. Nevertheless, chemical water quality and LQ did not co-vary substantially (correlation coefficients for different water quality variables ranged between −0.09 and 0.27; Leps et al., 2015). With the scope of this study being focused on informing stream restoration practice on promising spatial prioritization strategies, we did not consider chemical water quality issues in the context of this study, as these variables are normally not addressed in the context of hydromorphological stream restoration projects.

2.3. Data analysis

To analyze the effect of LQ and RQ on EQC, analysis of variance was used. In a first step, individual effects of LQ and RQ were tested, and in a second step a model using both independent variables LQ and RQ was run, also including the interaction term LQ × RQ. To further disentangle the relative contribution of LQ and RQ on EQC, we used a variance partitioning procedure, based on partial regression (due to the univariate dependent variable). We ran this using the "varpart" procedure in the R package "vegan" (Oksanen et al., 2013). In all these models, EQC was used as the dependent variable. The values of RQ in Hesse ranged between 2.6 and 6.8. To determine the effects of LQ on EQC at different RQ settings, the RQ values were divided into three quality categories for this analysis. The class boundaries were taken over from the German standard habitat survey scheme. Values of RQ < 3.5 comprise the quality classes undisturbed to moderately disturbed for which the term "good RQ" is used in this study (n = 17), RQ values in the range between 3.5 and 5.4 comprise the quality classes clearly to heavily disturbed, for which the term "intermediate RQ" was used in this study (n = 779) and values of RQ > 5.4 reflect quality classes very heavily to totally disturbed, for which the term "poor RQ" is used here (n = 291). To examine the effect of LQ on EQC in each of the RQ separately, individual regressions were applied. To test for the effects of unequal number of sites, power tests were performed (Appendix B). These tests demonstrated that the demonstrated patterns were largely independent of unequal number of sites.

To analyze the metacommunity patterns that may be driving the relationship between LQ, RQ and EQC, species richness (number of species per site) and diversity of individual communities as well as beta diversity and species co-occurrence patterns between communities within the 5-km radius were examined. Differences in species richness and Simpson's diversity between RQ categories were tested with Kruskal–Wallis tests followed by pairwise Mann–Whitney post-hoc comparisons. As a measure of beta diversity of the three RQ categories, we tested for homogeneity of dispersion (PERMDISP2; Anderson, 2006) with the "betadisper" function in "vegan" (Oksanen et al., 2013), based on Bray-Curtis distances. We assessed species co-occurrence patterns, by checking for checkerboarding in the site-by-species matrix, using the widely used C-score index (Stone and Roberts, 1990). The C-score gives the average number of checkerboards between all species pairs across the entire site-by-species matrix. Higher C-scores than expected

by chance indicate species segregation, whereas low scores indicate species aggregation or co-occurrence. To assess this we used the "nestedchecker" function in the "vegan" package and simulated null matrices using the "oecosimu" function. We generated 5000 null matrices to compare the observed C-score against and converted these C-scores to a standardized z-score. Null matrices were constrained by fixing both species richness of a site and species ranges. We used the "quasiswap" algorithm (Miklós and Podani, 2004) to produce the random matrices. Before creating the 5000 random matrices, we ran 50,000 "burn-ins" of initial swaps.

To examine potential spatial autocorrelation for each RQ class and whether LQ or spatial configuration were more important in determining EQC, we ran partial mantel tests, using the "mantel" function in "vegan". These were based two distance matrices, created using the Euclidian distance metric. First, geographic distance was calculated using Euclidean distance of the site geographic coordinates. Second, habitat distance was calculated based on a distance matrix of site-based LQ values. Partial mantel tests allowed for the differentiation of the effect of either space or LQ, whilst partialling out the influence of the other variable.

Statistical analyses were performed using the Statistica and R software packages (StatSoft, 2008; R Development Core Team, 2011).

3. Results

Analyzing the effects of LQ and RQ on EQC separately, a significant effect of each of them was detected (Fig. 2), but RQ (EQC = 0.8 RQ − 5.5, $r^2 = 0.27$, $p < 0.001$) explained approximately twice as much variation in the data as did LQ (EQC = 0.3 LQ + 1.9, $r^2 = 0.13$, $p < 0.001$). Partitioning the variation in EQC between LQ and RQ simultaneously demonstrated that a substantial proportion of variance previously explained by LQ is actually explained by the shared influence of LQ and RQ (Fig. 3). Separating RQ into the three classes good, intermediate and poor helped understanding the relationship between LQ, RQ and EQC. Considering both LQ, RQ and their interactive effect in one model, much of the shared variability of LQ and RQ is taken over by the interactive effect (Table 1, Fig. 4). A significant effect of LQ on EQC only remained in areas of intermediate RQ (Fig. 5). In areas of good or poor RQ, a significant relationship between LQ and ECQ was no longer observed, but EQC was simply a constant determined by RQ. EQC was spatially autocorrelated in intermediate and poor regional quality habitats, evident for both the full and pure effect after partialling out LQ (Table 2). However, considering pure effect of LQ, after partialling out geographic distance, showed the same results as the GLM approach, with significant effects of LQ only at sites situated in intermediate RQ areas.

Significantly higher species richness and diversity were found at sites within good RQ areas compared to medium and low (Fig. 6A-B; richness: Kruskal–Wallis test $\chi^2 = 97.0$, df = 2, $p < 0.001$; Simpson's D: Kruskal–Wallis test $\chi^2 = 74.9$, df = 2, $p < 0.001$). Beta dispersion between sites was marginally, but not significantly, different between the three RQ classes (Fig. 6C; Kruskal–Wallis test $\chi^2 = 5.8$, df = 2, $p = 0.054$), but by trend, dispersion appeared the lowest in good RQ areas. All three RQ categories exhibited significant checkerboarding in species distributions ($p < 0.001$). Checkerboarding was highest in intermediate RQ areas, with a significantly higher level of segregation than expected by chance ($p < 0.001$), with lower rates of segregation (closer to random but still highly significant) in LQ and HQ areas (Fig. 6D).

4. Discussion

The results of this study supported our hypothesis that EQC of benthic invertebrate communities depends more strongly on hydromorphological RQ at the 5 km scale than on hydromorphological LQ at the local 100 m scale. Hydromorphological habitat conditions at larger than local scale are, therefore, fundamental to the EQC of benthic
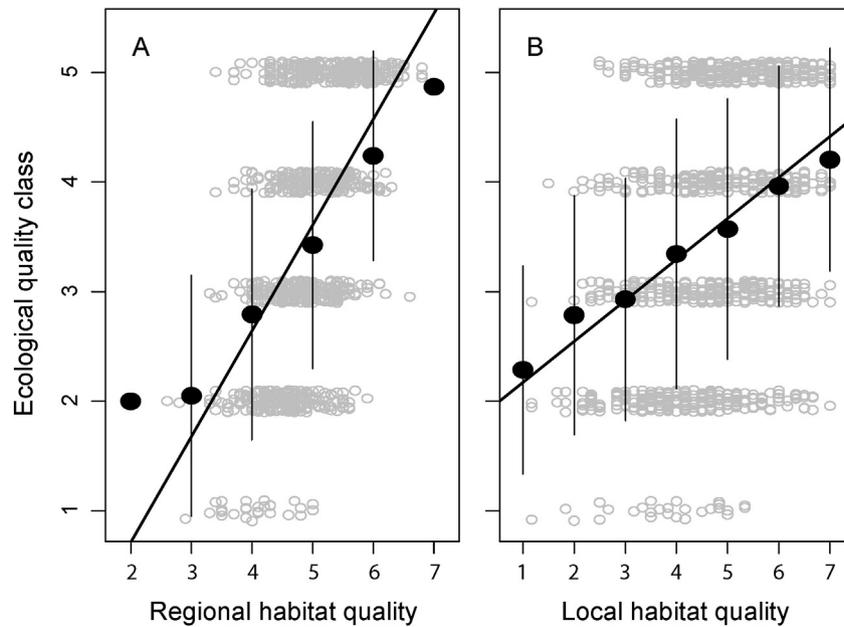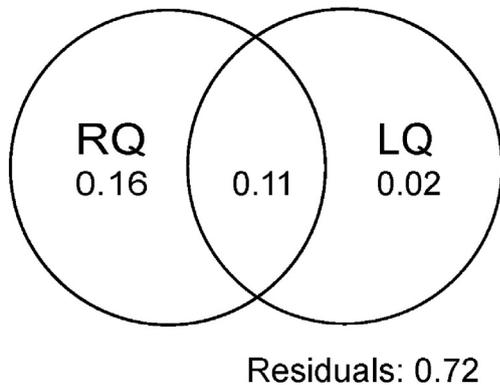
Fig. 2. Effects of (A) regional hydromorphological habitat quality (RQ); (B) local hydromorphological habitat quality (LQ) on the ecological quality class (EQC) of benthic invertebrates. The regressions are based on individual data points (gray circles). Black points and error bars indicate mean ± SD of EQC for each RQ and LQ class from 2 to 7 and 1–7, respectively.

invertebrate communities. Previous studies that addressed the issue of identifying the spatial scales that determine communities in streams have yielded inconsistent results. Johnson et al. (2007) found for several freshwater organisms (fish, benthic invertebrates, macrophytes, benthic diatoms) that environmental variables at the local scale of 20–100 m explained a greater share of community structure than environmental variables at the catchment scale. Also Sandin and Johnson (2004) emphasized the importance of the local scale (here: 50 m) for benthic invertebrate communities. However, their studies did not use the same set of variables describing local and regional habitat settings, as the local scale contained chemical parameters and substrate composition, whereas the regional scale contained land use and catchment geology.

In contrast, other studies emphasized the role of the regional scale for benthic invertebrate communities. For instance, Feld and Hering (2007) showed that meso-scale hydromorphological variables characterizing the 250–500 m surroundings explained a higher proportion of variability in local benthic invertebrate communities than local habitat variables at the 50–100 m scale. Townsend et al. (2003) found that environmental variables at the catchment scale were most successful in accounting for variation in macroinvertebrate assemblages, but also

variables at the reach (here: 230 m) and site scale (here: 30 m) were useful to both explain and predict macroinvertebrate communities. Focusing on the effects of the habitat quality of upstream reaches for local downstream communities, Lorenz and Feld (2013) and Kail and Hering (2009) showed that effects can be detected up to a distance of 5 km.

In these previous studies, the examination of the effects of habitat quality parameters on communities at the local scale was kept separate from the examination of the effect of these parameters on communities at the regional scale. In our study, we found that local and regional effects simultaneously and interactively influence benthic invertebrate communities. Benthic invertebrate communities could be explained only by considering habitat quality at both local and regional spatial scales simultaneously. This finding calls for a greater consideration of ecological theory in restoration. Metacommunity theory is especially helpful for explaining (and even forecasting) restoration outcomes (Lake et al., 2007; Brown et al., 2011). According to the "environmental filter" theory, local biodiversity is always a subset of regional biodiversity (Poff, 1997; Lake et al., 2007). Whether a local population of a species will become established depends on both the local environmental conditions and the condition of the metapopulation (Thompson and Townsend, 2006; Grenouillet et al., 2008; Brown et al., 2011), which in turn is affected by the regional environmental settings (Poff, 1997; Labbe and Fausch, 2000). In areas of good RQ, a high local diversity of benthic invertebrates was also maintained at sites with poor LQ. This likely reflects the fact that a well-established metacommunity with abundant and well-connected source populations can exert a mass effect that decouples species occurrence patterns from local habitat conditions, including rescue effects on local populations that would otherwise not be able to persist at all (Brown and Kodric-Brown, 1977; Dunning et al., 1992; Leibold et al., 2004).
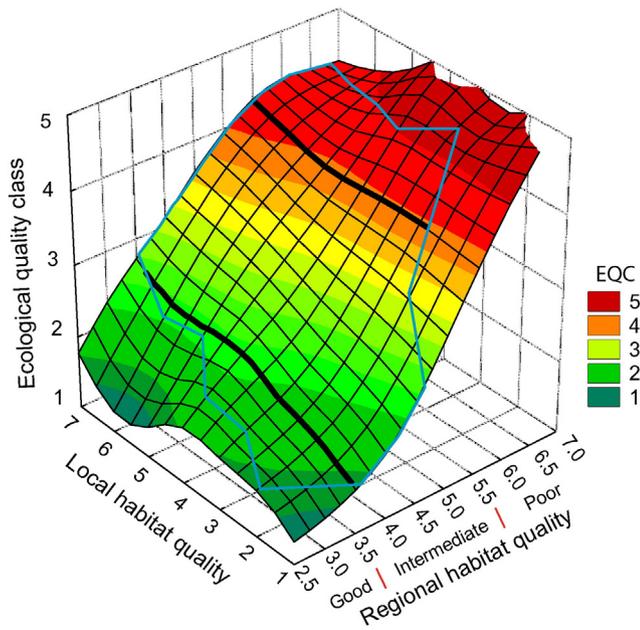

Fig. 3. Results of the variance partitioning of the effects of regional hydromorphological habitat quality (RQ) and local hydromorphological habitat quality (LQ) on the ecological quality class (EQC) of benthic invertebrates.
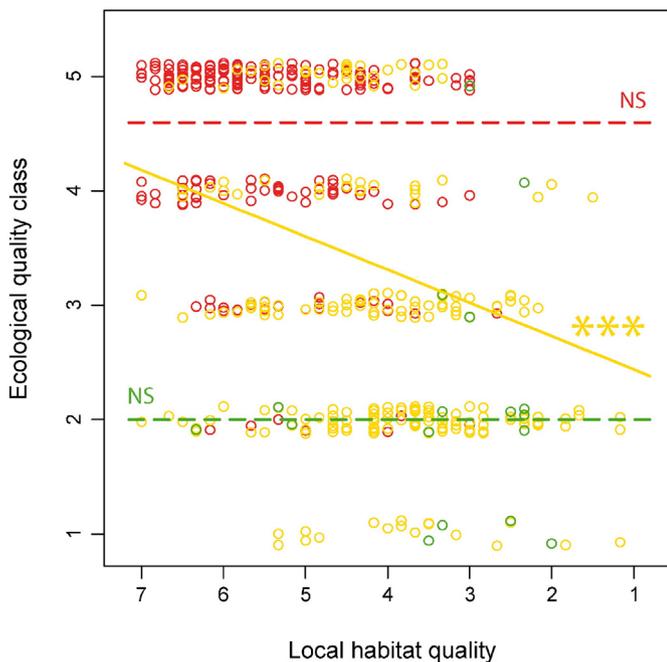
Table 1
Results from the full-factorial general linear model with ecological quality class (EQC) as dependent variable and local hydromorphological habitat quality (LQ) and regional hydromorphological habitat quality (RQ) as predictor variables. $R^2 = 0.22$, $n = 1087$. Significant results ($p < 0.05$) are given in bold.

Variable	SQ	df	F	p
LQ		1	0.67	0.41
RQ	24.26	2	10.48	**<0.001**
LQ × RQ	12.17	21	5.26	**<0.005**

Fig. 4. Response surface plot illustrating the relationship between ecological quality class (EQC), local hydromorphological habitat quality and regional hydromorphological habitat quality (RQ). Black lines separate "good" (RQ < 3.5), "intermediate" (3.5 ≤ RQ ≤ 5.4) and "poor" (RQ > 5.4) RQ classes. The blue boundary indicates the range of observed values. Color visualizes the EQC gradient from 1(high community quality, dark green) to 5 (bad community quality, red).

Our results support this theory, as the, by trend, lower beta dispersion found in good RQ communities indicates that species turnover between sites is lower than the intermediate and poor RQ zones. This lends some support to the idea that mass effects is the dominant paradigm driving community composition in good RQ areas, overriding the more commonly found metacommunity paradigm of species sorting (Cottenie, 2005). Previous stream studies have found a higher

Fig. 5. Interaction plot of the relationship between ecological quality class (EQC) and local hydromorphological habitat quality (LQ), for each of the three regional hydromorphological habitat quality (RQ) classes "good" (green; EQC = 2.0, R^2 = 0), "intermediate" (yellow; EQC = 0.3 LQ + 2.1, R^2 = 0.07, $p < 0.001$) and "poor" (red; EQC = 4.6, R^2 = 0).

Table 2
Results from the full and partial Mantel tests examining spatial autocorrelation of the ecological quality class (EQC) of benthic invertebrate communities, as well as the link between the pure effects of geographic distance and local hydromorphological habitat quality (LQ) on EQC. For the pure effects of geographic distance and LQ, LQ and geographic distance were partialled out, respectively. Significant results (p < 0.05) are given in bold.

RQ	Distance (full)		Distance (pure)		LQ (pure)	
	r	p	r	p	r	p
Good	−0.08	0.62	−0.11	0.64	−0.25	0.99
Intermediate	0.02	**0.012**	0.02	**0.010**	0.04	**0.001**
Poor	0.22	**0.001**	0.22	**0.001**	0.03	0.19

importance of mass effects in more highly connected mainstems of stream networks compared to more isolated headwaters (Brown and Swan, 2010). It is also feasible that this occurs through more densely occupied species pools with adequate dispersal and connectivity, as is likely occurring here in good RQ areas in our study.

Our assumption that co-occurrence patterns would be disrupted by habitat modification (i.e. from good to poor RQ) was not entirely supported. Checkerboarding did, in fact, decrease from intermediate to poor RQ sites, but also good RQ sites were less segregated. This contrasts recent findings that increasing environmental stress removes segregation between species (Larsen and Ormerod, 2014) and also decouples the linkages between taxonomic groups (Tonkin et al., 2016; online early). It is important to bear in mind the lower sample number of sites in good RQ areas may be influencing these patterns, thus these patterns need to be interpreted carefully. The low number of good RQ sites reflects the fact that these areas have become rare in Hesse (HMULV, 2000). However, previous studies have also suggested that mass/rescue effects from surrounding populations were responsible for the maintenance of good ecological status even in locally degraded habitats (Kail and Hering, 2009; Gellert et al., 2012; Lorenz and Feld, 2013).

In contrast, in regions of poor RQ, filter effects on biodiversity at greater spatial scales can explain why, even at local sites of high LQ, comparatively low levels of EQC were still found in benthic invertebrate communities (Poff, 1997; Kail and Wolter, 2013). Communities in poor RQ areas were depauperated and had the lowest diversity, indicating dispersal limitation was likely limiting local community assembly. This outcome is in accordance with the findings by Sundermann et al. (2011) and Lorenz and Feld (2013) that dispersal of benthic invertebrates is primarily limited to the 5-km surrounding or even shorter distances (Tonkin et al., 2014), and that potential colonizers originally located beyond this distance have a negligible effect on communities at restored sites. Nevertheless, dispersal distances of individual species that form macroinvertebrate communities vary greatly (Li et al., 2015), and metacommunity properties are also known to vary with stream network position (Brown and Swan, 2010). Thus, any fixed delimitation of a relevant colonist source zone can only be an approximation useful for management purposes.

Lower segregation in poor RQ than intermediate RQ communities indicates that assembly of species is more random than deterministic, potentially indicating they are not structured by a clear environmental gradient, nor by competitive interactions (Gotelli and McCabe, 2002; Horner-Devine et al., 2007). However, these patterns do not necessarily indicate that biotic interactions are being disrupted, as co-occurrence patterns can be driven through a variety of manners including for example interspecific competition (Diamond, 1975), historical or neutral factors (Ulrich, 2004), and environmental heterogeneity (or habitat checkerboards) (Bell, 2001; Heino, 2013; McCreadie and Bedwell, 2013). Specifically the latter mechanism can be highly scale dependent and particularly relevant at larger spatial scales in stream systems (Heino and Grönroos, 2013). Furthermore, it is likely that both habitat heterogeneity and dispersal mode interact to influence co-occurrence patterns in streams (Heino, 2013). Thus, not only may these patterns be driven by a weakening of biotic interactions, but also through a
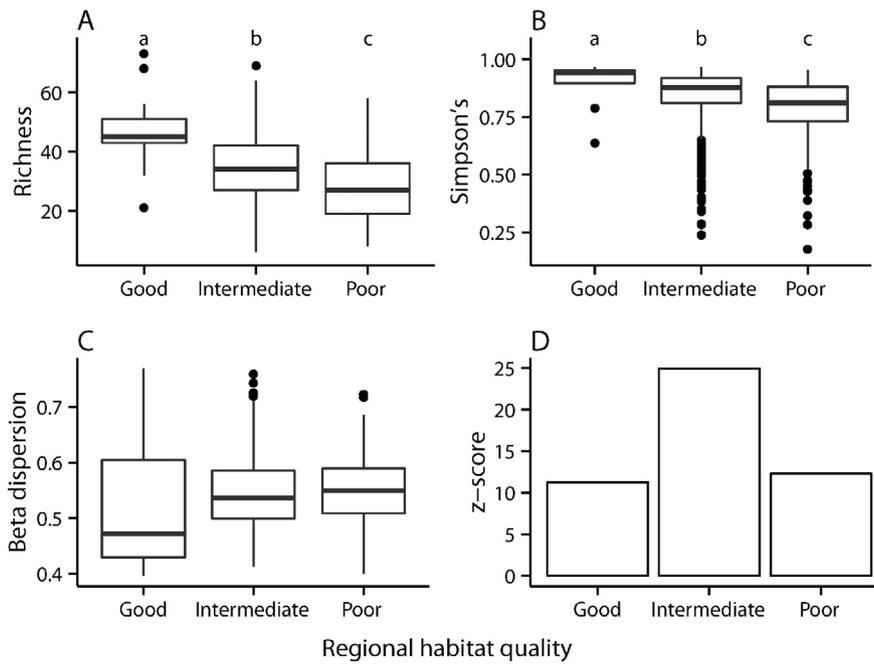
Fig. 6. Metacommunity structure in good, intermediate and poor regional hydromorphological stream habitat quality with respect to (A) species richness, (B) Simpson's Index of community diversity, (C) beta dispersion and (D) degree of checkerboarding (z-score). Shared letters in (A) and (B) indicate homogenous groups according to pairwise post-hoc comparison tests.

homogenization of habitat structure leading to a more random assembly process.

It has previously been suggested that stream fragmentation by artificial barriers might play an important role in limiting the spatial extent over which populations interact (Ward and Stanford, 1995; Pringle, 1997; Sundermann et al., 2011). A recent study, however, has concluded that artificial barriers (from small culverts, ground sills and slides to cascades and small dams) most likely have a limited effect on the dispersal of benthic invertebrates and that distance is more important in structuring benthic invertebrates in Central Europe (Tonkin et al., 2014). Only in areas of intermediate RQ did LQ show a substantial effect in determining EQC. Equivalently, the strongest species segregation occurred in communities in intermediate RQ areas, indicating that these communities were structured to the highest degree, likely either by competition or habitat segregation, or both. Based on these findings, we assumed that at least an intermediate regional habitat quality is required to establish a functional metacommunity network. Under such conditions, the propagule pressure of the species populations in surrounding stream reaches were sufficient to allow for species establishment at suitable sites. At the same time, this propagule pressure was too low to produce frequent rescue and spill-over effects at sites that cannot sustain species populations locally in the long term.

5. Conclusions and recommendations for restoration managers

The results of our study shed light on the interplay of hydromorphological habitat quality at the local and regional scale in determining benthic invertebrate communities and have direct implications for stream restoration practice. Our results suggest that beside known issues like the effects of multiple stressors (Leps et al., 2015) and the selection the most effective restoration methods (Pander et al., 2015; Simaika et al., 2015), improved spatial prioritization strategies for restoration projects can help to increase the effectiveness of stream restorations. Currently stream restoration efforts aim primarily to enhance habitat quality at the local reach scale in many individual projects. Our study suggests that this is a promising approach particularly in areas of overall intermediate regional habitat quality, where EQC is related to LQ. Hence, restorations in such areas of intermediate RQ combine

the potential for rapid community recovery, low risk of project failure, and moderate expenditures. Furthermore, with a few concerted upgrades of local environmental conditions, intermediate-quality regions may even be enhanced to overall good regional environmental conditions. Such concerted enhancements of habitat quality at the regional scale offer the potential to generate mass effects that will, additionally, exert positive influences on remaining non-restored low-quality reaches in the region (Kail and Hering, 2009; Gellert et al., 2012).

In areas of overall poor habitat quality, however, restoration concepts should address large spatial units, as in poor RQ areas short individual local high-quality reaches, at least for the short term, will not commonly support high-quality communities (Kail and Wolter, 2013; Lorenz and Feld, 2013). Currently, most restoration projects are conducted in such areas of poor RQ, and most of them to date have centered on the reach scale (Bernhardt et al., 2005; Roni et al., 2008; Palmer et al., 2010). Applied individually, these are the restoration projects that have a high likelihood to have limited beneficial effects on communities.

A less frequent case may be restorations occurring in areas of overall high RQ. In such areas, restoring the few reaches of low local habitat quality may be desirable for aesthetic reasons but are not prioritized in terms of ecological considerations.

Recent studies have advocated creating well-spaced, near natural stream reaches to facilitate species dispersal and colonization of restored river habitats (Kail and Hering, 2009; Gellert et al., 2012). For such high-quality reaches within degraded stream systems, the term "stepping stones" has been coined (Gellert et al., 2012). In contrast to the "spreading-effect" (Kail and Hering, 2009) and "stepping stones" concept, in which few high-quality reaches are assumed to be sufficient to provide dispersal corridors for stream species, our results indicate that the overall regional habitat quality, not the existence of individual, well-spaced high-quality reaches, is decisive for restoration success.

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.scitotenv.2016.02.126.

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