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

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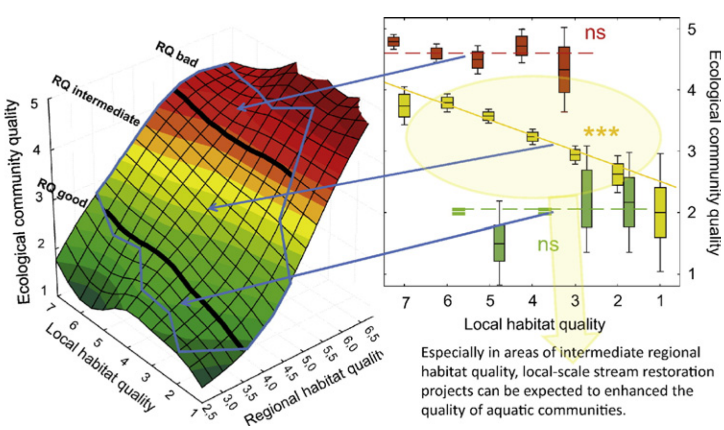
HIGHLIGHTS

- 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



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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;