A newly developed dispersal metric indicates the succession of benthic invertebrates in restored rivers

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Abstract

Dispersal capacity plays a fundamental role in the riverine benthic invertebrate colonization of new habitats that emerges following flash floods or restoration. However, an appropriate measure of dispersal capacity for benthic invertebrates is still lacking. The dispersal of benthic invertebrates occurs mainly during the aquatic (larval) and aerial (adult) life stages, and the dispersal of each stage can be further subdivided into active and passive modes. Based on these four possible dispersal modes, we first developed a metric (which is very similar to the well-known and widely used saprobic index) to estimate the dispersal capacity for 528 benthic invertebrate taxa by incorporating a weight for each mode. Second, we tested this metric using benthic invertebrate community data from a) 23 large restored river sites with improvements of river bottom habitats dating back 1 to 10 years, b) 23 unrestored sites, and c) 298 adjacent surrounding sites in the low mountain and lowland areas of Germany. We hypothesize that our metric will reflect the temporal succession process of benthic invertebrate communities colonizing the restored sites, whereas no temporal changes are expected in the unrestored and surrounding sites. By applying our metric to these three river treatment categories, we found that the average dispersal capacity of benthic invertebrate communities in the restored sites significantly decreased in the early years following restoration, whereas there were no changes in either the unrestored or the surrounding sites. After all taxa had been divided into quartiles representing weak to strong dispersers, this pattern became even more obvious; strong dispersers colonized the restored sites during the first year after restoration and then significantly decreased over time, whereas weak dispersers continued to increase. The successful application of our metric to river restoration might be promising in further applications of this metric, for example, in assessments of rivers or metacommunity structure.

Key words: integrated dispersal metric, weight approach, macroinvertebrate, community succession, river restoration.

Highlights

We develop a new dispersal metric for river ecosystems.

We test our metric using 23 restoration projects in Germany.

Our metric successfully elucidates community succession in restored rivers.

Strong and weak dispersers show an inverse successional trend in restored rivers.

Our metric is useful to detect environmental perturbation and community succession.

1. Introduction

In the natural state, many ecosystems are characterized by frequent disturbances that result in a dynamic environmental mosaic. This process is being enhanced by unprecedented global change (e.g., human disturbance, habitat fragmentation, pollution, and climate warming) on a local, regional or global scale, which is especially true for river ecosystems (Revenga et al., 2005; Xenopoulos et al., 2005). However, whether and how an organism's colonization capacity enables it to cope with new challenges is unclear. Colonization is a series of processes that includes population dispersal, establishment, and reproduction (Wirth et al., 2008). As a key attribute, dispersal capacity, which is a measure of the frequency and distance of an organism's movement among different habitats, can greatly influence community dynamics (Beisner et al., 2006; Heino, 2013). This topic has been well studied in terrestrial and marine ecosystems (Bowler & Benton, 2005; Clobert et al., 2012; Grantham et al., 2003; Kinlan & Gaines, 2003; Lester et al., 2007). Although information on dispersal traits is also available for a certain number of fish (Pépino et al., 2012; Radinger & Wolter, 2014; Stoll et al., 2013) and benthic invertebrates from freshwater ecosystems (Furse et al., 2006; Kappes & Haase, 2012; Schmidt-Kloiber & Hering, 2015; Tachet et al., 2010), no simple metric that can express the dispersal capacity of a community exists. As a result, the application of community succession theory to freshwater ecosystems has not been widely addressed yet (Milner et al., 2008).

Due to the diversity in life cycles, a direct measurement of dispersal capacity is notoriously difficult for functionally important organism groups in freshwater ecosystems, such as benthic invertebrates (Bredervel et al., 2011; Hughes, 2007). Most benthic invertebrates live at the bottom of a river channel (aquatic habitats) and sometimes move overland (aerial habitats), such as the adult stages of most aquatic insects (Bilton et al., 2001; Bohonak & Jenkins, 2003). For the aquatic dispersal mode, passive drift (with the aid of external water flow, wind, or animal vectors) and active movement (self-generated) along the river bottom are of particular importance, whereas for the aerial dispersal mode, the active flight (upstream) and the passive wind drift of adult aquatic insects predominate (Bilton et al., 2001). Benthic invertebrates with life cycles restricted to aquatic habitats show weaker dispersal capacities, whereas those with a flying adult stage tend to be stronger dispersers (Hughes, 2007; Kappes & Haase, 2012; Miller et al., 2002). In addition to life cycle stages, the relative importance of dispersal via active or passive modes also differs among taxonomic groups. These various mobility and life cycle characteristics make benthic invertebrates an ideal model group for conducting comprehensive ecological studies of river ecosystems.

Recently, considerable advancement has been achieved through the compilation of a certain number of dispersal trait attributes (at the genus level) into databases, for instance the STAR (Standardization of River Classifications) project (www.eu-star.at; Furse et al., 2006), the www.freshwaterecology.info database (Schmidt-Kloiber & Hering, 2015), and the Freshwater Invertebrates: Taxonomy, Biology, Ecology (Tachet et al., 2010). The four major dispersal modes, aquatic active, aquatic passive, aerial active, and aerial passive, are incorporated into these databases (Bis & Usseglio-Polatera, 2004; Furse et al., 2006; Schmidt-Kloiber & Hering, 2015). However, each of these four modes may provide different dispersal aspects to a certain extent, and a comprehensive measure for quantifying integrated dispersal capacity is still lacking. Therefore, the main aim of our study is to build a metric by incorporating these four dispersal modes to represent an integrative assessment of dispersal capacity for several hundred riverine benthic invertebrates. The approach used to develop such a metric and the resulting formula is very similar to the well-known and widely used saprobic index (Kolkwitz & Marsson, 1909). The dispersal metric will be beneficial to future freshwater studies that investigate, for example, colonization or metacommunity structure.

River restoration provides an opportunity to test the suitability of our metric because restored rivers need to be (re-)colonized by benthic invertebrates following restoration. This colonization process particularly depends on the dispersal capacity of benthic invertebrates: species with a high dispersal capacity are expected to colonize the restored sites first, whereas species with low dispersal capacities will show up much later. To investigate this pattern, we used riverine benthic invertebrate data from 23 large restored sites (Fig. 1) that have been undergoing restoration for a span of 1 to 10 years. These 23 restoration projects involved significant changes to the river bottom sediments, including removal of specimens. As we had data neither from these restored sites prior to restoration nor from the yearly monitoring performed subsequent to site restoration, we applied a space-for-time substitution approach, using each restoration as a temporal replicate. We compared the dispersal capacity values of the 23 restored sites with dispersal capacity values from 23 unrestored sites, each located in close proximity to one of the restored sites. As a second control group, we calculated the dispersal capacity values of all other available community data from the river sites in the nearby surroundings (< 5 km) of the restoration projects. This 5-km surrounding area has been shown to be the relevant species source pool for the colonization of restored sites (Stoll et al., 2014; Stoll et al., 2013; Sundermann et al., 2011a; Sundermann et al., 2011b).

Based on this study design and using our new developed metric, we calculated an average dispersal capacity value for the 23 benthic invertebrate communities in the restored sites, the 23 communities in the nearby unrestored sites, and the 298 communities from the 5-km surroundings. These data enabled us to test the following hypotheses: 1) the average dispersal metric of benthic invertebrate communities decreases over time at restored sites, whereas no such changes can be observed in the unrestored and surrounding sites, and 2) species that are strong dispersers are expected to rapidly colonize the restored sites, whereas weak dispersers need more time to colonize the restored sites and thus are expected to increase continuously in the early post-restoration stage.

2. Materials and methods

2.1. Dispersal capacity

The STAR database (www.eu-star.at; Furse et al., 2006) comprises information on four major dispersal modes (aquatic active, aquatic passive, aerial active and aerial passive) for 528 benthic invertebrates taxa (Table S1). Yet, information on active and passive terrestrial dispersal (e.g. overland crawling) is missing in this and other databases. There are only a few studies quantifying terrestrial dispersal distances as terrestrial dispersal is a comparatively rare event in benthic invertebrate species (Flecker & Allan, 1988; Hershey et al., 1993). Due to the missing information and low relevance of terrestrial dispersal for most benthic invertebrates, our dispersal metric is based on the most common aquatic and aerial modes only.

In the STAR database, an integer is assigned describing the affinity of each taxon to the four dispersal modes, ranging from 0 (no affinity) to 3 (high affinity). The simplest way to calculate an overall species-specific dispersal capacity metric (*sDCM*) for a given species is to sum up the dispersal capacity values of the four dispersal modes (aquatic active, aquatic passive, aerial active, and aerial passive) of the respective species. This *sDCM* could be converted into a standardized *sDCM* (*standsDCM*), which ranges between 0 and 1, using the minimum-maximum rescaling approach (equation 1).

$$standsDCM = \frac{((aqa_i + aqp_i + aea_i + aep_i) - min_c)}{(max_c - min_c)} \qquad (1)$$

where *standsDCM* refers to the standardized species dispersal capacity metric, aqa_i refers to the aquatic active dispersal mode of species *i*, aqp_i refers to the aquatic passive dispersal mode, aea_i refers to the aerial active dispersal mode, and aep_i refers to the aerial passive dispersal mode, min_c refers to the value at which the sum of assigned dispersal capacity values was lowest within the whole community *c* (n = 528), and max_c refers to the value at which the sum of assigned dispersal capacity values was highest.

For example, *Haplotaxis gordioides* (Oligochaeta) has 1 point for the aquatic passive mode, respectively, but 0 points for aerial active, passive and aquatic active, resulting in a low value for *standsDCM* (i.e., 0.0) using equation 1. In contrast, *Hydropsyche saxonica* (Trichoptera) has 2, 3, 3, and 1 points for aquatic active, aquatic passive, aerial active, and aerial passive, respectively, leading it to a high value of *standsDCM* (i.e., 1.0).

Yet, for the majority of benthic invertebrate species, the aerial dispersal distance is greater than the aquatic dispersal distance (Minshall & Petersen, 1985). For example, when water velocity was approximately 50 cm s^{-1}, nymphs of *Hydropsyche* spp. could drift 11.5 m on average while *Baetis rhodani* travelled 4.4 m (Elliott, 1971). In contrast, the flight distance of adult Hydropsychidae along the Detroit River and Lake St. Clair in Canada averaged 1.8 km; as much as 5 km were recorded when light traps were used (Kovats et al., 1996). Half of the emerging *Baetis* in an Arctic stream flew at least 1.6 km upstream from their emergence sites (Hershey et al., 1993). Therefore, it is necessary to assign more weight to the aerial dispersal mode to increase the accuracy of an overall dispersal metric. To determine a suitable weight factor, we tested 30 different possible weight values for the aerial dispersal modes (1–30). A value of 1 referred to equal weights for aquatic and aerial modes, while 30 referred to a 30-fold weight for the aerial mode. Using these 30 different weight factors, we calculated a community dispersal capacity metric (*cDCM*) of a given sampling site as the average of the *standsDCMs* weighted by species abundance (Table S2). We tested the weighting approach using benthic invertebrate data from 23 river restoration projects in Germany ranging from 1 to 10 years after restoration (for more details please see the following sub-chapter). In total we made 30 regressions of each of the 10 years after restoration against the 30 dispersal capacity metrics (Fig. 2A). The most suitable weight value was 2, as it resulted in the regression model with the highest explanatory power and the lowest *P* value (Fig. 2 B). Accordingly, the most suitable overall species dispersal metric is as follows (equation 2):

$$standwsDCM = \frac{((aqa_i + aqp_i + 2 \times aea_i + 2 \times aep_i) - min_c)}{(max_c - \min_c)} \qquad (2)$$

where *standwsDCM* refers to the standardized weighted species dispersal capacity metric, aqa_i refers to the aquatic active dispersal mode of species *i*, aqp_i refers to the aquatic passive dispersal mode, aea_i refers to the aerial active dispersal mode, and aep_i refers to the aerial passive dispersal mode, min_c refers to the value at which the sum of assigned dispersal capacity values was lowest (min_c=1) within the whole community *c* (n = 528), and max_c refers to the value at which the sum of assigned dispersal capacity values was highest (max_c=13). For simplification reasons from here on, the standardized weighted species dispersal capacity metric (*standwsDCM*) will be referred as *sDCM*.

Based on this approach, an overall community dispersal capacity metric (*cDCM*) of a given sample, reflecting the relative composition of weak and strong dispersers, would be the average *sDCM* weighted by species abundance or presence/absence. The *cDCM* is calculated as follows (equation 3):

$$cDCM = \frac{\sum_{i=1}^{n} sDCM_i \times AP_{ij}}{\sum_{i=1}^{n} AP_{ij}} \qquad (3)$$

where *cDCM* refers to the community dispersal capacity metric at site *j*, $sDCM_i$ refers to the dispersal capacity metric of the species *i*, AP_{ij} refers to the abundance or presence of the species *i* at site *j*. The calculation mode of this new community dispersal capacity metric is very similar to the well-known and widely used saprobic index (Kolkwitz & Marsson, 1909). Both formulas include very similar variables: the abundance of a given species, a weighting factor and a value representing either the *sDCM* or the saprobic index of a given species, respectively.

2.2. Study system and data collection

The 23 large restoration projects selected for this study (Table S3, Fig. 1) were carried out between 1997 and 2007 in the low mountain and lowland areas (26–268 m above sea level) of Germany; all sites had been restored with the aim to improve the habitats, hydrological conditions, and species diversity. Principal measures consisted of the removal of bank fixation, creation of new watercourses, wood placement and broadening of rivers to create multichannel patterns (Stoll et al., 2013; Sundermann et al., 2011a; Sundermann et al., 2011b). All these 23 restoration projects involved significant changes of river bottom sediments and initially led to a significant removal of specimens and opening of new habitat for colonization, with the initial states following restoration being similar for all sites. Consequently, the evolution of the colonization process among these restoration projects is comparable. Benthic invertebrate community data were compiled from these 23 restored sites for our analyses. In addition, community data from two control groups, unrestored and surrounding, were used to differentiate the temporal colonization patterns of benthic invertebrate communities among these three river treatment categories. An unrestored site was assigned to each of the 23 restored sites. The 23 unrestored sites were selected because they represented the conditions of the restored sites prior to the restoration action, meaning all unrestored sites were degraded. The unrestored sites were located upstream of the corresponding restored site to avoid the influence of organisms drifting from the restored site. The mean distance between the paired restored and unrestored sites was 1 km. In each river, both restored and unrestored sites were similar in terms of geology, adjacent land use, river type, and catchment area. The surrounding sites were selected because they have been shown to be the species source pool for the colonization of restored sites up to a distance of 5 km away from the restored sites (Stoll et al., 2014; Stoll et al., 2013; Sundermann et al., 2011a; Sundermann et al., 2011b). Only river sites within the same catchment where the restoration project was conducted were considered for the surrounding site datasets, which resulted in 298 surrounding sites (ranging from 2 to 39 sites per project). A sketch map of the relative localities of the restored, unrestored, and surrounding sites is shown in Fig. S1.

Benthic invertebrates were collected from March to July in 2007 and 2008 in the restored and unrestored sites. Thus, the mean time period between restoration and our investigation ranged from 1–10 years. Because data from consecutive yearly monitoring for those river sites were not available, the space-for-time substitution approach was used to represent the riverine biological conditions during the 1–10 years. This is not generally the best method, and repeated sampling at the same restored site over several years would be more valuable in carrying out dispersal studies. Yet, due to a general lack of pre-restoration data, the substitution approach has been widely used in previous studies (Blois et al., 2013; Haase et al., 2013; Januschke et al., 2011; Leps et al., 2016; Lorenz et al., 2012; Lorenz et al., 2013; Stoll et al., 2013; Sundermann et al., 2011b). Sampling was carried out following the EU Water Framework Directive (WFD) compliant sampling protocol (Haase et al., 2004a; Haase et al., 2004b). Twenty multiple habitat samples were taken in each site within 200 m river reaches using a shovel sampler (25 × 25 cm sampling area and 500 µm mesh size). All benthic invertebrates were preserved in 70% ethanol and identified in the laboratory following the protocol of Haase et al. (2004a; 2004b). The organisms were identified to the genus or species level, except for Chironomidae, Naididae and Tubificidae, which were identified to the subfamily or family level. Based on the same sampling protocol data from the surrounding sites were collected by governmental environmental agencies of the federal states of Hesse and North Rhine-Westphalia from the same period of the year (March to July) during the period from 2004 to 2008. All analyses of benthic invertebrates in our study were based on both quantitative (abundance of a given species in one sampling site) and qualitative (presence/absence of a given species in one sampling site) data.

The multimetric index (MMI) of the EU Water Framework Directive compliant assessment system in Germany (Hering et al., 2010) was used to quantify the quality of the sites involved in our study. The correlation between MMI and *standcDCM* with abundance data showed a very weak correlation ($F_{1,67} = 4.72$, $R^2 = 0.07$, $P = 0.03$) when the sites of all three river treatment categories were combined, indicating that the potential differences in the habitat quality of restored, unrestored and surrounding sites do not have an effect on the average species' dispersal capacity at our studied sites.

2.3. Statistical analysis

The first hypothesis was that a significant temporal change in the *cDCM* of benthic invertebrates only occurs in the restored sites, and this was tested by plotting the *cDCM* at a given site as a function of time. Nonlinear regressions (inverse first order, equation 4) were used to extract the temporal trends of the *cDCM* of benthic invertebrates in the three river treatment categories. Inverse first order regression was selected because the recolonization of benthic invertebrates followed the rule of community succession, namely fast changes in the early period and then a long period of dynamic equilibrium. Similarly, inverse regressions were also used, e.g., to estimate the decomposition rate of leaf litter over time in river systems (Austin & Vitousek, 2000; Cusack et al., 2009).

$$y = y_0 + \frac{a}{x} \qquad (4)$$

where y refers to dependence (*cDCM*), y_0 refers to *cDCM* at time zero, a refers to correlation coefficient, and x refers to independence (years after restoration).

The second hypothesis was that strong dispersers rapidly colonize the restored sites while the colonization of weak dispersers is slow, and to test this, we arranged all taxa in an ascending order according to their dispersal metrics and then allocated them to four dispersal groups using a quartile approach. Taxa in the 1st quartile (Q1) were defined as weak dispersers, and taxa in the 4th quartile (Q4) were strong dispersers. Taxa in the 2nd and 3rd quartiles were categorized as weak to medium dispersers (Q2) and strong to medium dispersers (Q3), respectively (Table S1; Fig. 3A). For the three river treatment categories, the temporal changes of four dispersal groups in proportion were then made using inverse first order regressions.

3. Results

3.1. Dispersal metrics of various taxonomic groups

Similar results of estimated *sDCMs* were observed using abundance and presence/absence data, but only results evaluated with abundance data are shown here. Values of the *sDCMs* were lower for Oligochaeta and Turbellaria and higher for Ephemeroptera and Trichoptera (Fig. 3B). After splitting all taxa into four dispersal groups representing weak to strong dispersers, the value of the *sDCM* for each taxonomic group became more obvious; all taxa of Oligochaeta, Turbellaria, Hirudinea, Gastropoda, Crustacea, and Megaloptera were weak dispersers, whereas most of the Ephemeroptera and Trichoptera were strong dispersers (Fig. 4).

3.2. Ecological application of the dispersal metric

Overall, the *cDCM* of benthic invertebrates in the restored sites decreased significantly (abundance: $F_{1, 21} = 5.37$, $R^2 = 0.20$, $P = 0.03$; presence/absence: $F_{1, 21} = 8.49$, $R^2 = 0.29$, $P < 0.01$) during the 1–10 years after restoration

(Fig. 5), whereas no significant trends were observed in the unrestored and surrounding sites using both qualitative and quantitative data (Fig. 5).

Succession of the benthic invertebrate communities was observed in the restored sites over the 10–year period with weak and strong dispersers showing contrasting responses in the first half decade and later reaching dynamic equilibrium (Fig. 6A, B). Specifically, the strong dispersers rapidly colonized the restored sites in the first year after restoration, and the proportion of species richness attributable to them dramatically decreased from the second year following restoration onwards ($F_{1,\,21}$ = 9.00, R^2 = 0.30, P < 0.01; Fig. 6B). The proportion of weak dispersers in the communities significantly increased over the 10–year period (abundance: $F_{1,\,21}$ = 4.78, R^2 = 0.19, P = 0.04; species richness: $F_{1,\,21}$ = 7.48, R^2 = 0.26, P = 0.01; Fig. 6A, B). However, no significant trend was observed in the relative abundance of strong dispersers (Fig. 6A), nor was a significant trend noted for the weak to medium and strong to medium dispersers in either the quantitative and qualitative data (Fig. 6A, B). As expected, no changes were observed for the four types of dispersers in the unrestored and surrounding sites.

4. Discussion

4.1. Strengths, weaknesses and challenges in the dispersal traits of benthic invertebrates

In our study, we developed a dispersal capacity metric based on the widely used dispersal modes from the STAR database. Our metric provides an initial estimate of dispersal capacity of benthic invertebrates, and is valuable because our metric leads to the proper interpretation of community succession in the restored habitats. However, there is still a large number of species for which dispersal information is lacking (Bilton et al., 2001; Bohonak & Jenkins, 2003; Brederveld et al., 2011). In addition, the values from the STAR database and most other sources are based on expert judgements, and as such, prone to misinterpretation. To fill in these knowledge gaps, further real data on species dispersal capacities are needed so that more comprehensive analyses can be carried out in future studies.

The dispersal capacity of most benthic invertebrates is constrained in comparison to terrestrial organisms due to both the distinct boundaries of freshwater ecosystems and the often short-lived flying adult stages (Bohonak & Jenkins, 2003; Tonkin et al., 2014). In contrast, some recent genetic studies indicate that aerial dispersal over long distances within and across catchments may be common (Hughes, 2007; Miller et al., 2002), most likely by means of passive dispersal modes (Bohonak & Jenkins, 2003) or because the distance between the two adjacent headwaters is within the dispersal range of some flying adults (Geismar et al., 2015; Griffith et al., 1998). Nevertheless, these various studies are in line with the conclusion that in general the dispersal capacity of benthic invertebrates is remarkably stronger via air than via water. In our study, we took care of this general finding by doubling the weight of the aerial modes based on the statistical results of 30 regression models.

4.2. Dispersal in restored rivers

Our approach is based on the assumption that in undisturbed rivers, the community dispersal capacity metric (*cDCM*) of benthic invertebrates is stable and should not change over time, whereas in recently disturbed rivers, strong dispersers have higher probabilities of arriving earlier than weak dispersers, and thus, the *cDCM* of benthic invertebrates should change over time. This was reflected in our study design, which included restored, unrestored, and surrounding river treatment categories. By applying our metric to these three river treatment categories, a significant decrease in the *cDCM* of benthic invertebrates was observed in the restored sites, particularly in the first 3–5 years, whereas there were no significant trends in either the unrestored or the surrounding sites (Fig. 5), which supports our first hypothesis. In addition, a nonsignificant trend in the unrestored sites indicated that the *cDCM* of benthic invertebrates shows no remarkable differences among the restored sites prior to the restoration activities.

However, these results raise another question: Why was there a decrease in the *cDCM* of benthic invertebrates in the restored sites over time? To answer this question, we investigated the community succession of benthic invertebrates in the restored sites. Communities in the newly restored habitats were rapidly assembled by strong dispersers. Species with low dispersal capacity needed longer time to arrive at the restored sites. However, generally, species that are poor at dispersing tend to be better competitors once habitats have stabilized and, hence, replace the early arriving but less competitive strong dispersers. *Simulium* spp., for example, possess strong dispersal capacities, but other freshwater species outcompete and displace the *Simulium* spp. in the ongoing process of succession, which results in their absence or low abundance after a certain period of time (Downes & Lake, 1991). An increase in *Simulium* spp. following disturbance was also reported by Milner et al. (2008), who investigated Glacial Wolf Point Creek in Alaska between 1977 and 2005. Taxa with good dispersal capacity but poor competitive ability are defined as fugitive species (Horn & MacArthur, 1972; Milner et al., 2008). Beside *Simulium* spp., many other taxa also belong to fugitive species, such as the chironomids, *Cricotopus intersectus* (Milner et al., 2008) and *Baetis* spp. (Minakawa & Gara, 2003). Therefore, identification of the nonrandom establishment and persistence of strong and weak dispersers in the succession of communities answered the above question and also support our second hypothesis.

Although clear temporal trends of the entire benthic invertebrate communities in the restored sites were observed, the temporal trend of strong dispersers using abundance data was not significant. This is most likely because a few strongly dispersing individuals can colonize the restored sites in the early post-restoration stage, but they may not establish substantial populations in the short term. Such an effect can greatly influence the responses of communities to environmental changes, thereby leading to a relatively low proportional abundance of strong dispersers in the early stage and a nonsignificant trend in reduction over time.

Milner et al. (2008) noted that dispersal constraints largely influenced the community succession, as non-insect taxa required at least 20 years to colonize. In our case, the colonization speed of non-insect taxa (e.g., Oligochaeta, Turbellaria, Hirudinea, Gastropoda, and Crustacea) was slower than that of insect taxa (e.g., Ephemeroptera and Trichoptera). However, in comparison to the study conducted by Milner et al. (2008), the colonization speed was relatively high in our case, taking approximately 3–5 years for those non-insect taxa to colonize the restored sites in this temperate climatic region. Minshall et al. (1983) also reported that it took three years to obtain the full colonization of the original taxa in the Teton River (Idaho) following a major flash flood.

We are fully aware that no single mechanism can completely describe community succession. In addition to dispersal capacity, extrinsic (e.g., competition and landscape barriers) and intrinsic drivers (e.g., species' life cycles and parasite loads) are also of utmost importance (Grabner et al., 2014). Overall, our study provides a dispersal capacity metric that has proven to be a useful tool to assess riverine organism colonization patterns of new habitats after dramatic anthropogenic disturbances. By means of this metric, our study demonstrates that benthic invertebrate communities in new river habitats can rapidly develop, and the nonrandom succession of benthic invertebrate communities indicates that a period of 3–5 years is needed after restoration to reach equilibrium in terms of community dispersal capacity. To further improve our metric, direct measurements of dispersal frequency and distance for individual benthic invertebrates will be important. Beyond stimulating work to refine taxon-specific estimates of dispersal capacity, our dispersal capacity metric might be used in multiple ways. For example, this metric could be incorporated into conventional bioassessment indices that may improve the sensitivity of assessment indices to detect perturbations and increase the ability of assessment indices to explore changes in river benthic invertebrate communities. It may also allow for further investigation into the precise role of dispersal capacities in shaping metacommunities in headwaters and main streams or at larger spatial scales to allow for scrutiny of potential differences between highland and lowland communities.

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References

Austin, A.T., Vitousek, P.M., 2000. Precipitation, decomposition and litter decomposability of *Metrosideros polymorpha* in native forests on Hawai'i. J. Ecol. 88, 129–138.

Beisner, B.E., Peres-Neto, P.R., Lindström, E.S., Barnett, A., Longhi, M.L., 2006. The role of environmental and spatial processes in structuring lake communities from bacteria to fish. Ecology 87, 2985–2991.

Bilton, D.T., Freeland, J.R., Okamura, B., 2001. Dispersal in freshwater invertebrates. Ann. Rev. Ecol. Syst. 32, 159–181.

Bis, B., Usseglio-Polatera, P., 2004. Species Traits Analysis. Standardisation of river classifications: Framework method for calibrating different biological survey results against ecological quality classifications to be developed for the Water Framework Directive. http://www.eu-star.at/pdf/Deliverable_N2.pdf.

Blois, J.L., Williams, J.W., Fitzpatrick, M.C., Jackson, S.T., Ferrier, S., 2013. Space can substitute for time in predicting climate-change effects on biodiversity. Proc. Natl. Acad. Sci. U.S.A. 110, 9374–9379.

Bohonak, A.J., Jenkins, D.G., 2003. Ecological and evolutionary significance of dispersal by freshwater invertebrates. Ecol. Lett. 6, 783–796.

Bowler, D.E., Benton, T.G., 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. Biol. Rev. 80, 205–225.

Brederveld, R.J., Jähnig, S.C., Lorenz, A.W., Brunzel, S., Soons, M.B., 2011. Dispersal as a limiting factor in the colonization of restored mountain streams by plants and macroinvertebrates. J. Appl. Ecol. 48, 1241–1250.

Clobert, J., Baguette, M., Benton, T.G., Bullock, J.M., 2012. Dispersal Ecology and Evolution. Oxford University Press, Oxford, UK.

Cusack, D.F., Chou, W.W., Yang, W.H., Harmon, M.E., Silver, W.L., 2009. Controls on long-term root and leaf litter decomposition in neotropical forests. Global Change Biol. 15, 1339–1355.

Downes, B.J., Lake, P.S., 1991. Different colonization patterns of two closely related stream insects (*Austrosimulium* spp.) following disturbance. Freshwater Biol. 26, 295–306.

Elliott, J.M., 1971. The distances travelled by drifting invertebrates in a lake district stream. Oecologia 6, 350–379.

Flecker, A.S., Allan, J.D., 1988. Flight direction in some Rocky Mountain mayflies (Ephemeroptera), with observations of parasitism. Aquat. Insects 10, 33–42.

Furse, M., Hering, D., Moog, O., Verdonschot, P., Johnson, R., Brabec, K., et al., 2006. The STAR project: context, objectives and approaches. Hydrobiologia 566, 3–29.

Geismar, J., Haase, P., Nowak, C., Sauer, J., Pauls, S.U., 2015. Local population genetic structure of the montane caddisfly *Drusus discolor* is driven by overland dispersal and spatial scaling. Freshwater Biol. 60, 209–221.

Grabner, D.S., Schertzinger, G., Sures, B., 2014. Effect of multiple microsporidian infections and temperature stress on the heat shock protein 70 (hsp70) response of the amphipod *Gammarus pulex*. Parasit. Vectors 7, 170.

Grantham, B.A., Eckert, G.L., Shanks, A.L., 2003. Dispersal potential of marine invertebrates in diverse habitats. Ecol. Appl. 13, 108–116.

Griffith, M.B., Barrows, E.M., Perry, S.A., 1998. Lateral dispersal of adult aquatic insects (Plecoptera, Trichoptera) following emergence from headwater streams in forested Appalachian catchments. Ann. Entomol. Soc. Am. 91, 195–201.

Haase P., Hering D., Jähnig S.C., Lorenz A.W., Sundermann A., 2013. The impact of hydromorphological restoration on river ecological status: a comparison of fish, benthic invertebrates, and macrophytes. Hydrobiologia 704, 475–488.

Haase, P., Lohse, S., Pauls, S., Schindehütte, K., Sundermann, A., Rolauffs, P., Hering, D., 2004a. Assessing streams in Germany with benthic invertebrates: development of a practical standardised protocol for macroinvertebrate sampling and sorting. Limnologica 34, 349–365.

Haase, P., Pauls, S., Sundermann, A., Zenker, A., 2004b. Testing different sorting techniques in macroinvertebrate samples from running waters. Limnologica 34, 366–378.

Heino, J., 2013. Does dispersal ability affect the relative importance of environmental control and spatial structuring of littoral macroinvertebrate communities? Oecologia 171, 971–980.

Hering, D., Borja, A., Carstensen, J., Carvalho, L., Elliott, M., Feld, C.K., et al., 2010. The European Water Framework Directive at the age of 10: a critical review of the achievements with recommendations for the future. Sci. Total Environ. 408, 4007–4019.

Hershey, A.E., Pastor, J., Peterson, B.J., Kling, G.W., 1993. Stable isotopes resolve the drift paradox for *Baetis* mayflies in an Arctic River. Ecology 74, 2315–2325.

Horn, H.S., MacArthur, R.H., 1972. Competition among fugitive species in a Harlequin environment. Ecology 53, 749–752.

Hughes, J.M., 2007. Constraints on recovery: using molecular methods to study connectivity of aquatic biota in rivers and streams. Freshwater Biol. 52, 616–631.

Januschke K., Brunzel S., Haase P., Hering D., 2011. Effects of stream restorations on riparian mesohabitats, vegetation and carabid beetles. Biodivers. Conserv. 20, 3147−3164.

Kappes, H., Haase P., 2012. Slow, but steady: Dispersal velocity and strategies of freshwater mollusks. Aquat. Sci. 74, 1–14.

Kinlan, B.P., Gaines, S.D., 2003. Propagule dispersal in marine and terrestrial environments: a community perspective. Ecology 84, 2007–2020.

Kolkwitz R., Marsson M., 1909. Ökologie der tierischen saprobien. Int. Rev. Hydrobiol. 2, 126−152.

Kovats, Z.E., Ciborowski, J.J.H., Corkum, L.D., 1996. Inland dispersal of adult aquatic insects. Freshwater Biol. 36, 265–276.

Leps M., Sundermann A., Tonkin J.D., Lorenz A.W., Haase P., 2016. Time is no healer: increasing restoration age does not lead to improved benthic invertebrate communities in restored river reaches. Sci. Total Environ. 557-558, 722−732.

Lester, S.E., Ruttenberg, B.I., Gaines, S.D., Kinlan, B.P., 2007. The relationship between dispersal ability and geographic range size. Ecol. Lett. 10, 745–758.

Lorenz, A.W., Korte, T., Sundermann, A., Januschke, K., Haase, P., 2012. Macrophytes respond to reach-scale river restorations. J. Appl. Ecol. 49, 202–212.

Lorenz, A.W., Stoll, S., Sundermann, A., Haase, P., 2013. Do adult and YOY fish benefit from river restoration measures? Ecol. Eng. 61, 174–181.

Miller, M.P., Blinn, D.W., Keim, P., 2002. Correlations between observed dispersal capabilities and patterns of genetic differentiation in populations of four aquatic insect species from the Arizona White Mountains, U.S.A. Freshwater Biol. 47, 1660–1673.

Milner, A.M., Robertson, A.L., Monaghan, K.A., Veal, A.J., Flory, E.A., 2008. Colonization and development of an Alaskan stream community over 28 years. Front. Ecol. Environ. 6, 413–419.

Minakawa, N., Gara, R.I., 2003. Effects of chum salmon redd excavation on benthic communities in a stream in the Pacific Northwest. Trans. Am. Fish. Soc. 132, 598–604.

Minshall, G.W., Andrews, D.A., Manuel-Faler, C.Y., 1983. Application of island biogeographic theory to streams: macroinvertebrate recolonization of the Teton River, Idaho. In: Barnes, J.R., Minshall, G.W. (Eds.), Stream Ecology: Application and Testing of General Ecological Theory. Springer Press, pp. 279–297.

Minshall, G.W., Petersen, R.C., 1985. Towards a theory of macroinvertebrate community structure in stream ecosystems. Arch. Hydrobiol. 104, 49–76.

Pépino, M., Rodríguez, M.A., Magnan, P., 2012. Fish dispersal in fragmented landscapes: a modeling framework for quantifying the permeability of structural barriers. Ecol. Appl. 22, 1435–1445.

Radinger, J., Wolter, C., 2014. Patterns and predictors of fish dispersal in rivers. Fish Fish. 15, 456–473.

Revenga, C., Campbell, I., Abell, R., De Villiers, P., Bryer, M., 2005. Prospects for monitoring freshwater ecosystems towards the 2010 targets. Philos. Trans. R. Soc. B-Biol. Sci. 360, 397–413.

Schmidt-Kloiber A., Hering D., 2015. www.freshwaterecology.info – An online tool that unifies, standardises and codifies more than 20,000 European freshwater organisms and their ecological preferences. Ecol. Indic. 53, 271–282.

Stoll, S., Sundermann, A., Lorenz, A.W., Kail, J., Haase, P., 2013. Small and impoverished regional species pools constrain colonization of restored river reaches by fishes. Freshwater Biol. 58, 664–674.

Stoll, S., Kail, J., Lorenz, A.W., Sundermann, A., Haase, P., 2014. The importance of the regional species pool, ecological species traits and local habitat conditions for the colonization of restored river reaches by fish. PloS ONE 9, e84741.

Sundermann, A., Antons, C., Cron, N., Lorenz, A., Hering, D., Haase, P., 2011a. Hydromorphological restoration of running waters: effects on benthic invertebrate assemblages. Freshwater Biol. 56, 1689–1702.

Sundermann, A., Stoll, S., Haase, P., 2011b. River restoration success depends on the species pool of the immediate surroundings. Ecol. Appl. 21, 1962–1971.

Tachet, H., Richoux, P., Bournaud, M., Usseglio-Polatera, P., 2010. Invertebres d'Eau Douce. Systematique, Biologie, Ecologie. CNRS Editions, Paris, France.

Tonkin, J.D., Stoll, S., Sundermann, A., Haase, P., 2014. Dispersal distance and the pool of taxa, but not barriers, determine the colonisation of restored river reaches by benthic invertebrates. Freshwater Biol. 59, 1843–1855.

Wirth, C., Lichstein, J.W., Dushoff, J., Chen, A., Chapin, F.S., 2008. White spruce meets black spruce: dispersal, postfire establishment, and growth in a warming climate. Ecol. Monogr. 78, 489–505.

Xenopoulos, M.A., Lodge, D.M., Alcamo, J., Marker, M.D., Schuulze, K., van Vuuren, D.P., 2005. Scenarios of freshwater fish extinctions from climate change and water withdrawal. Global Change Biol. 11, 1–8.

Figure legends

Fig. 1. Geographic locations of the restoration projects and their surrounding sites in the low mountain and lowland areas of Germany. Unrestored sites were not shown in the figure because the mean distance between the paired restored and unrestored sites was 1 km, and all restored and unrestored sites were overlapped at the defined spatial scale. The full names of the restored sites are given in Table S3.

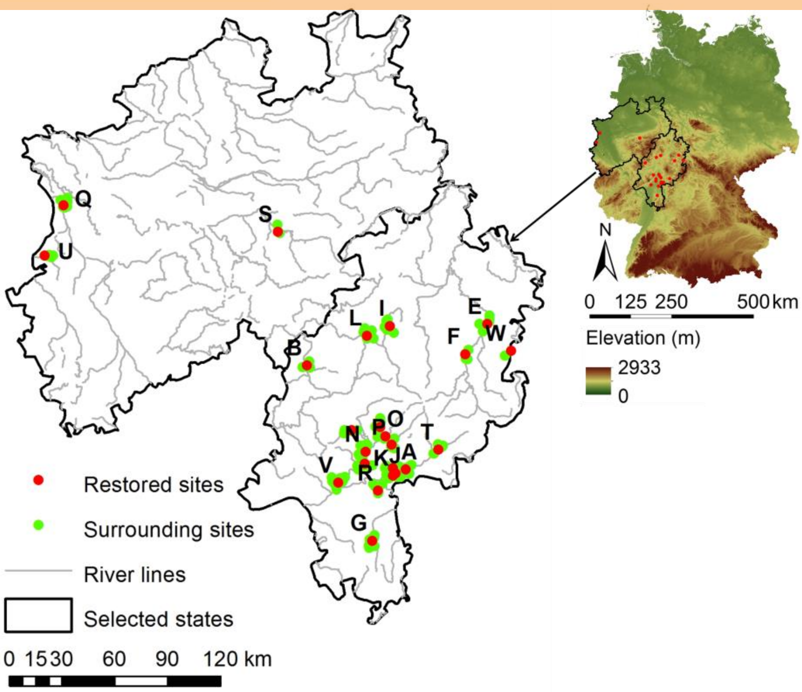
Fig. 2. The 10-year trends in the standardized community dispersal capacity metric (*standcDCM*) of benthic invertebrates in 23 restored sites. In total, 30 curves in (A) are displayed with partial overlap, referring to 30 weights (1−30) of aerial dispersal modes with abundance data. The R^2 and P value of each regression model are presented in (B).

Fig. 3. Summary plots of the standardized species dispersal capacity metrics (*standsDCM*) for (A) 528 species and (B) 15 taxonomic groups with low to high dispersal capacity. The classification of the four dispersal groups is based on the weight calculated with abundance data, i.e., 2 in (A). Four dispersal groups are defined by a quartile approach: weak dispersers = 0–25th; weak to medium dispersers = 25th–50th; strong to medium dispersers = 50th–75th; and strong dispersers = 75th–1. The dot refers to the mean value, the whisker refers to the standard error, and the number above and below the whisker refers to the number of species on which the calculation is based in (B). The full names of taxonomic groups are given in Fig. 4.

Fig. 4. The proportion of the species richness among the four dispersal groups for each taxonomic group.

Fig. 5. The 10-year trends in the standardized community dispersal capacity metric (*standcDCM*) of benthic invertebrates in the restored, unrestored, and surrounding sites using (A) abundance and (B) presence/absence data.

Fig. 6. The 10-year trends in proportion of abundance and species richness of the four dispersal groups in the restored sites using (A) abundance and (B) presence/absence data. The trends in the unrestored and surrounding sites are not presented because they are not significant. The four dispersal groups are defined by a quartile approach: weak dispersers = 0–25th; weak to medium dispersers = 25th–50th; strong to medium dispersers = 50th–75th; and strong dispersers = 75th–1.



502

503 **Fig. 1.**

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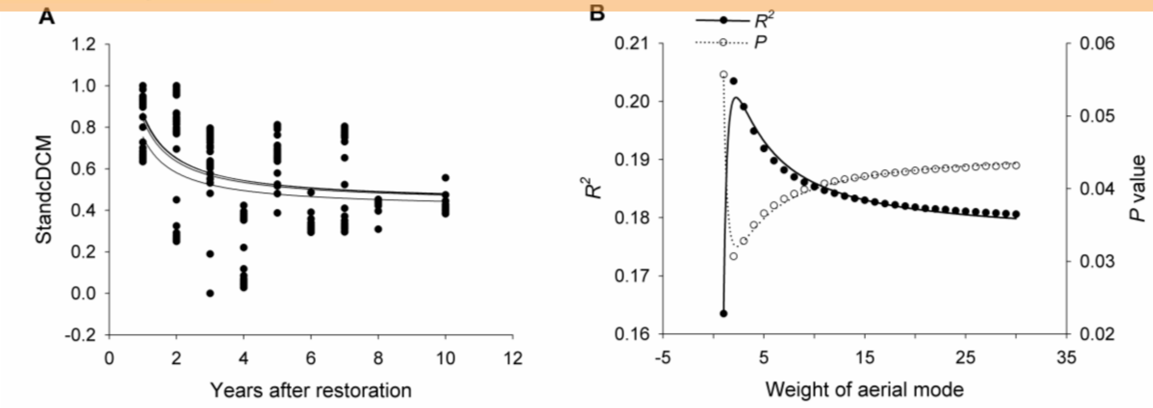

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506 **Fig. 2.**

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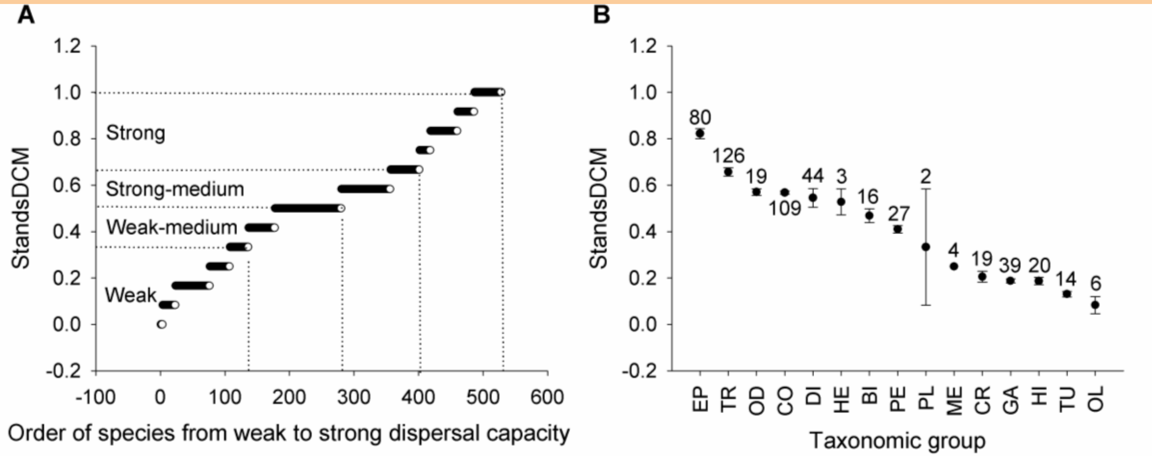
A
StandsDCM
Strong
Strong-medium
Weak-medium
Weak
Order of species from weak to strong dispersal capacity
B
StandsDCM
80
126
19
109
44
3
16
27
2
4
19
39
20
14
6
EP TR OD CO DI HE BI PE PL ME CR GA HI TU OL
Taxonomic group

Fig. 3.

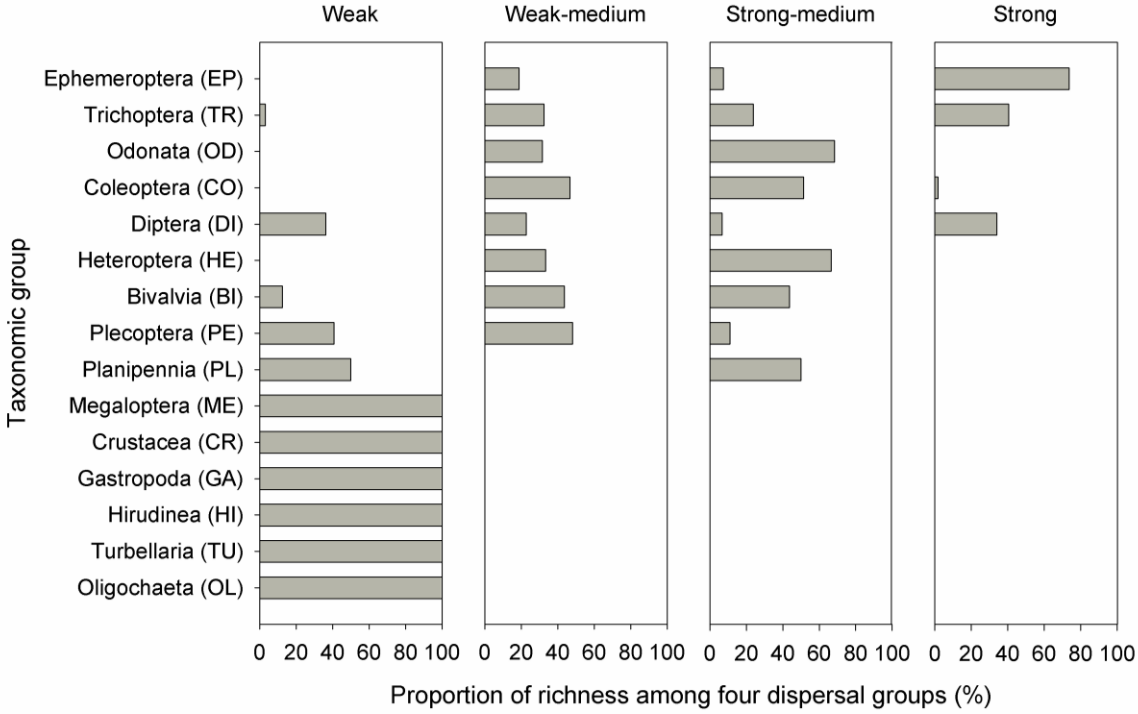
Weak
Weak-medium
Strong-medium
Strong
Taxonomic group
Ephemeroptera (EP)
Trichoptera (TR)
Odonata (OD)
Coleoptera (CO)
Diptera (DI)
Heteroptera (HE)
Bivalvia (BI)
Plecoptera (PE)
Planipennia (PL)
Megaloptera (ME)
Crustacea (CR)
Gastropoda (GA)
Hirudinea (HI)
Turbellaria (TU)
Oligochaeta (OL)
0 20 40 60 80 100
Proportion of richness among four dispersal groups (%)

Fig. 4.

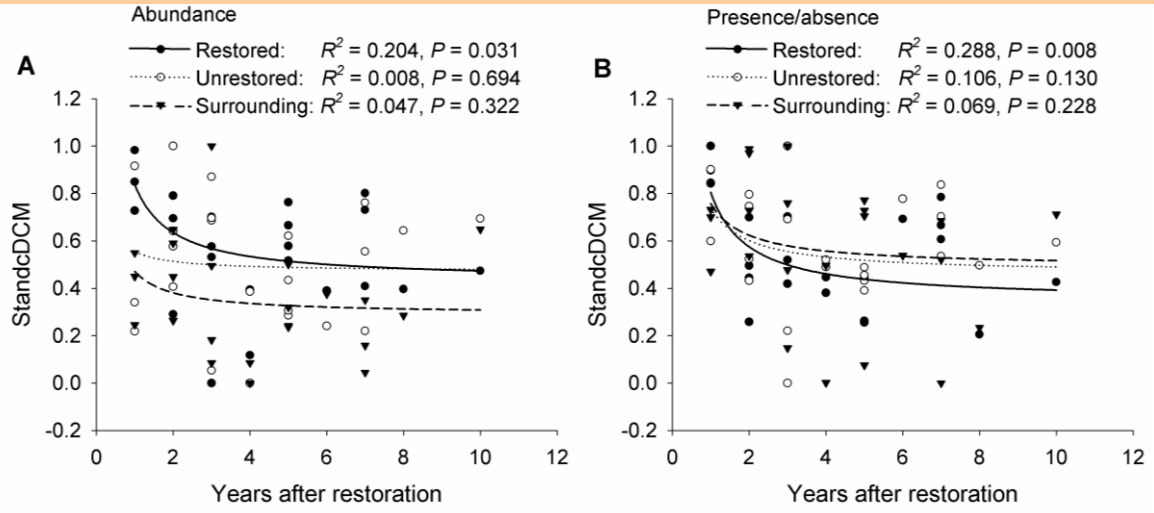
A
Abundance
Restored: R^2 = 0.204, P = 0.031
Unrestored: R^2 = 0.008, P = 0.694
Surrounding: R^2 = 0.047, P = 0.322
StandcDCM
Years after restoration
B
Presence/absence
Restored: R^2 = 0.288, P = 0.008
Unrestored: R^2 = 0.106, P = 0.130
Surrounding: R^2 = 0.069, P = 0.228
StandcDCM
Years after restoration

Fig. 5.

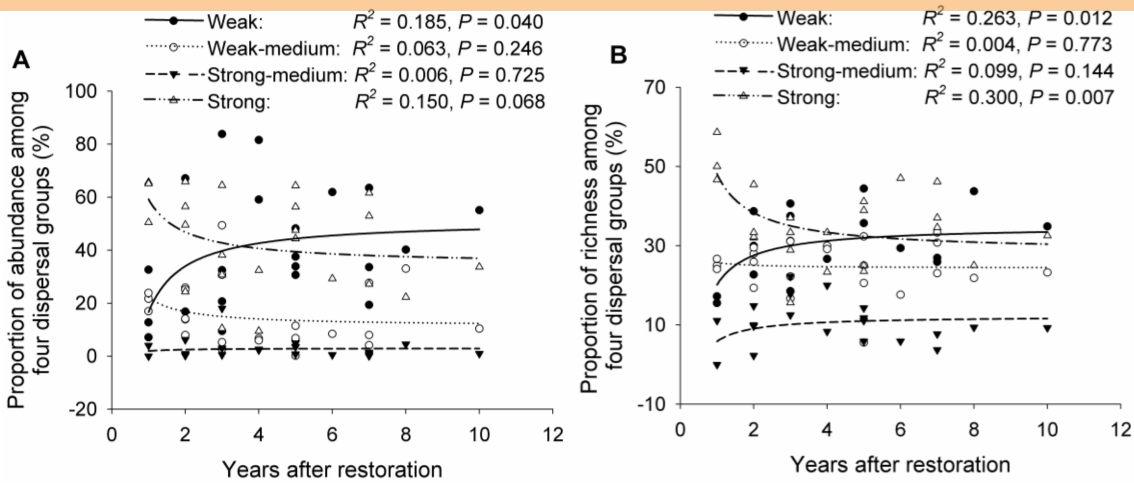
A
Weak: R^2 = 0.185, P = 0.040
Weak-medium: R^2 = 0.063, P = 0.246
Strong-medium: R^2 = 0.006, P = 0.725
Strong: R^2 = 0.150, P = 0.068
Proportion of abundance among four dispersal groups (%)
Years after restoration
B
Weak: R^2 = 0.263, P = 0.012
Weak-medium: R^2 = 0.004, P = 0.773
Strong-medium: R^2 = 0.099, P = 0.144
Strong: R^2 = 0.300, P = 0.007
Proportion of richness among four dispersal groups (%)
Years after restoration

Fig. 6.

Supplementary

Table S1. Values of the four dispersal modes and the standardized species dispersal capacity metric (*sDCM*), based on the weight of aerial dispersal mode calculated with abundance data, i.e., 2, as well as the group information for 528 species of benthic invertebrates using a quartile approach. A positive integer, ranging from 0 (no affinity) to 3 (high affinity), is assigned to each taxon and describes the affinity to each dispersal mode. The *sDCM* ranges between 0 and 1 and is produced using the minimum-maximum rescaling approach. Gen. refers to general family group; Ad. refers to the adult; and Lv. refers to the larval. All information is available in the attached Adobe Acrobat file.

Table S2. Statistical results (R^2) of the standardized community dispersal capacity metric of benthic invertebrates in the restored, unrestored, and surrounding sites based on the following weights of aerial dispersal modes: 1–10, 15, 20, 25, and 30. Instead of all weights of 10−30, only 15, 20, 25, and 30 are involved in the table because there are no significant changes when the different weights are incorporated. Rest. = Restored, Unre = Unrestored, Surr = Surrounding, Q1 = weak, Q2 = weak to medium, Q3 = strong to medium, and Q4 = strong dispersers. The results of the four dispersal groups in these three river treatment types are identical when the weight exceeds 4. **indicates $P < 0.01$ and *indicates $P < 0.05$.

Table S3. Characteristics of 23 restored sites in the low mountain and lowland areas of Germany.

Fig. S1. Sketch map of the relative localities of the restored, unrestored, and surrounding sites.