A newly developed dispersal capacity 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 life stage can be further subdivided into active and passive modes. Based on these four possible dispersal modes, we first developed a simple metric 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.

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 (Grantham et al., 2003; Kinlan and Gaines, 2003; Bowler and Benton, 2005; Lester et al., 2007; Clobert et al., 2012). Although information on dispersal traits is also available for a certain number of fish (Pépino, 2012; Stoll et al., 2013; Radinger and Wolter, 2014) and benthic invertebrates from freshwater ecosystems (e.g., Furse et al., 2006; Tachet et al., 2010; Kappes and Haase, 2012; Schmidt-Kloiber and Hering, 2012), 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 (Hughes, 2007; Brederveld et al., 2011). 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 and 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 (Miller et al., 2002; Hughes, 2007, Kappes and Haase, 2012). 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 and Hering, 2012), 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 and Usseglio-Polatera, 2004; Furse et al., 2006; Schmidt-Kloiber and Hering, 2012). 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 simple metric by incorporating these four dispersal modes to represent an integrative assessment of dispersal capacity for several hundred riverine benthic invertebrates. This 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 (Sundermann et al., 2011a, b; Stoll et al., 2013, 2014).

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.

Materials and methods

Dispersal capacity

We selected four dispersal modes, i.e., aquatic active, aquatic passive, aerial active, and aerial passive, to determine an integrative measure of dispersal capacity for each of the 528 benthic invertebrates that were available from the 641 studied taxa in the STAR database (Table S1). Some individuals may disperse by walking over the ground, for example, *Gammarus*, thus exhibiting terrestrial dispersal, which is dissimilar to the common aquatic and aerial means of dispersal used by most benthic invertebrates. For most riverine benthic invertebrates, however, there are only a few studies quantifying the minimum terrestrial dispersal distances (Flecker and Allan, 1988; Hershey et al., 1993), and there is no database available to quantify terrestrial dispersal. We assume that terrestrial dispersal does not greatly contribute to the overall dispersal capacity of benthic invertebrates.

For the majority of benthic invertebrates, the aerial dispersal distance is greater than the aquatic dispersal distance (Minshall and 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). The average flight distance of adult hydropsychidae along the Detroit River and Lake St. Clair in Canada was 1.8 km, even 5 km in some cases with the light trap collection (Kovats et al., 1996), and half of the emerging *Baetis* in an Arctic stream might travel 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 our metric. In our study, we estimated the suitable assigned weight using the following approaches. First, 30 weights of the aerial dispersal modes (1–30) were selected to represent 30 candidates of the species dispersal metric (SDM), where the value of 1 referred to equal weights for aquatic and aerial modes, and 30 referred to the highest candidate weight of the aerial mode. Second, the community dispersal metric (CDM) of a given sampling site reflected the relative composition of weak and strong dispersers. They were calculated for a given sampling site as the average of SDM weighted by species abundance or presence/absence (equation 1). CDM were then converted into standardized CDM (standCDM), which ranged between 0 and 1, using the minimum-maximum rescaling approach. Third, we made 30 regressions of years after restoration against the candidate standCDM (Fig. 2A, C). The most suitable weight was selected as the one with the highest explanatory power and the lowest *P* value. The statistical results showed that the highest explanatory power and lowest *P* value occurred when the weight was 2 using abundance data (Fig. 2 B), while the increase in the explanatory power and the decrease in the *P* values were maintained until the weight reached 10 using presence/absence data (Fig. 2D). Although we used 10 as the weight for the presence/absence data, we should note that there were no significant changes incorporating larger weights (Table S2). Consequently, we presented our dispersal metrics for abundance (equation 2) and presence/absence data (equation 3) with the following equations:

$$standCDM = \frac{\sum_{i=1}^{n} SDM_i \times AP_{ij}}{\sum_{i=1}^{n} AP_{ij}} \qquad (1)$$

$$SDM\_abund = aqa \times 1 + aqp \times 1 + aea \times 2 + aep \times 2 \qquad (2)$$

$$SDM\_pres/abs = aqa \times 1 + aqp \times 1 + aea \times 10 + aep \times 10 \qquad (3)$$

where *standCDM* refers to the standardized community dispersal metric at site *j*, *SDM* refers to the dispersal metric of the species *i*, *AP* refers to the abundance or presence of the species *i* at site *j*, *SDM_abund* refers to the species dispersal metric for abundance data, *SDM_pres/abs* refers to the species dispersal metric for presence/absence data, *aqa* refers to the dispersal capacity of species *i* via aquatic active mode, *aqp* refers to the aquatic passive mode, *aea* refers to the aerial active mode, and *aep* refers to the aerial passive mode.

In the STAR database, a positive integer, ranging from 0 (no affinity) to 3 (high affinity), is assigned to each taxon, which describes its affinity to each dispersal mode. For example, *Haplotaxis gordioides* (Oligochaeta) has 1 point for aquatic active and passive modes, respectively, but 0 points for both aerial active and passive, resulting in a low value for standardized SDM (standSDM) (i.e., 0.08) using equation 2 and the minimum-maximum rescaling approach (Table S1) and an assignment to the group of weak dispersers, whereas *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 standSDM, (i.e., 1.00) (Table S1) and an assignment to the group of strong dispersers.

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 diversities. Principal measures consisted of the removal of bank fixation, creation of new watercourses, wood placement and broadening of rivers to create multichannel patterns (Sundermann et al., 2011a, b; Stoll et al., 2013). 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, and 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 the two control groups, unrestored and surrounding, were used to differentiate the temporal colonization patterns of benthic invertebrate communities among these three river treatment categories. Each of the 23 restored sites was assigned an unrestored site. 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 (Sundermann et al., 2011a, b; Stoll et al., 2013, 2014). 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. However, the substitution approach has been widely used in previous studies (Sundermann et al., 2011b; Lorenz et al., 2012, 2013; Haase et al., 2013; Stoll et al., 2013; Blois et al., 2014). Sampling was carried out following the EU Water Framework Directive (WFD) sampling protocol (Haase et al., 2004a, b). 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, b). 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. Following the same sampling protocol as for the above restored and unrestored sites, data from the surrounding sites were collected by governmental environmental agencies of the 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 standCDM 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.

Statistical analysis

The first hypothesis was that a significant temporal change in the standCDM of benthic invertebrates only occurs in the restored sites, and this was tested by plotting the standCDM 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 standCDM 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 and Vitousek, 2000; Cusack et al., 2009).

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

where y refers to dependence (standCDM), y_0 refers to standCDM 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.

Results

Dispersal metrics of various taxonomic groups

Similar results of estimated standSDMs were observed using abundance and presence/absence data, but only results evaluated with abundance data are shown here. Values of the standSDMs 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 standSDM 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).

Ecological application of the dispersal metric

Overall, the standCDM of benthic invertebrates in the restored sites decreased significantly (abundance: $F_{1, 21}$ = 5.37, R^2 = 0.20, P = 0.03; presence/absence: $F_{1, 21}$ = 11.65, R^2 = 0.36, 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: $F_{1, 21}$ = 4.35, R^2 = 0.17, P = 0.05; 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.

Discussion

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

In our study, we developed a simple dispersal 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 it is valuable because our metric leads to the proper interpretation of community succession in the restored habitats. An investigation of the literature indicates that dispersal traits are available for some benthic invertebrates, but there are still a large number of species for which dispersal information is lacking (Bilton et al., 2001; Bohonak and Jenkins, 2003; Brederveld et al., 2011). Based on the available knowledge of dispersal from various sources, each species' dispersal mode is assigned a positive integer between 0 and 3 in the STAR database (Furse et al., 2006). However, those values are 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 short-lived flying adult stages (Bohonak and 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 (Miller et al., 2002; Hughes, 2007), most likely by means of passive dispersal modes (Bohonak and Jenkins, 2003) or because the distance between the two adjacent headwaters is within the dispersal range of some flying adults (Griffith et al., 1998; Geismar et al., 2015). Nevertheless, these various studies are in line with the conclusion that the dispersal capacity of benthic invertebrates is remarkably stronger via air than via water. In our study, we selected the suitable weight based on the statistical results of 30 regression models. A higher weight with presence/absence data indicated that a species' flying capacity is considerable more important than its aquatic drifting capacity. This stems from the assumption of the regression model that a good model shows higher dispersal capacity in the early stages following restoration activities and lower values in the latter stages. Increasing the weight of the aerial dispersal mode can therefore considerably increase the proportion of strong dispersers and further enlarge the value of the metric in the early stage, which results in a higher explanatory power. In some extreme cases, the contribution of the aquatic mode to the metric can be ignored if the aerial weight is large enough (e.g., > 30). However, the clear bell curves indicated a relative lower weight using abundance data. This suggests that the importance of an aquatic mode cannot be ignored because most benthic invertebrates spend their lives under the water for a considerable length of time (Hughes, 2007; Brederveld et al., 2011).

Dispersal in restored rivers

Our approach is based on the assumption that in undisturbed rivers, the standCDM 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 standCDM 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 standCDM 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 standCDM 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 standCDM 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 and 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 and 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 and 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 simple dispersal metric that has proven to be a useful tool to assess riverine organism colonization 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., 2014. Space can substitute for time in predicting climate-change effects on biodiversity. Proc. Natl. Acad. Sci. U.S.A. (In press).

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., 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.

Haase, P., Hering, D., Jähnig, S.C., Lorenz, A.W., Sundermann, A., 2013. How does ecological status respond to river restoration? A comparison of fish, benthic invertebrates, macrophytes and hydromorphology. Hydrobiologia 704, 475–488.

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.

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.

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

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. and 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., 2012. www.freshwaterecology.info - the taxa and autecology database for freshwater organisms, version 5.0 (accessed on 15-01-2013).

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 metric (standCDM) of benthic invertebrates in 23 restored sites. In total, 30 curves are displayed with partial overlap, referring to 30 weights (1−30) of aerial dispersal modes with (A) abundance and (C) presence/absence data. The R^2 and P value of each regression model are presented in (B, D).

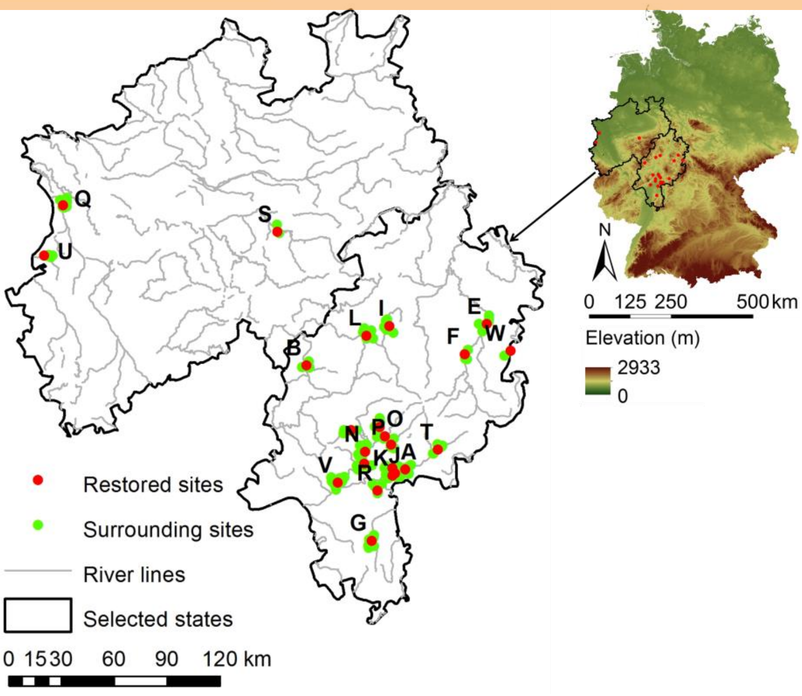
Fig. 3. Summary plots of the standardized species dispersal metrics (standSDM) for (A) 528 species and (B) 15 taxonomic groups with low to high dispersal capacity. The classification of the four dispersal groups is based on the weight calculated with abundance data, i.e., 2 in (A). Four dispersal groups 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 metric (standCDM) of benthic invertebrates in the restored, unrestored, and surrounding sites using (A) abundance and (B) presence/absence data. The weights of abundance and presence/absence data are 2 and 10, respectively, for the standardized species dispersal metric.

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.


Q
S
U
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B
P
O
N
T
K
J
A
V
R
G
N
0 125 250 500 km
Elevation (m)
2933
0
● Restored sites
● Surrounding sites
River lines
Selected states
0 15 30 60 90 120 km

Fig. 1.

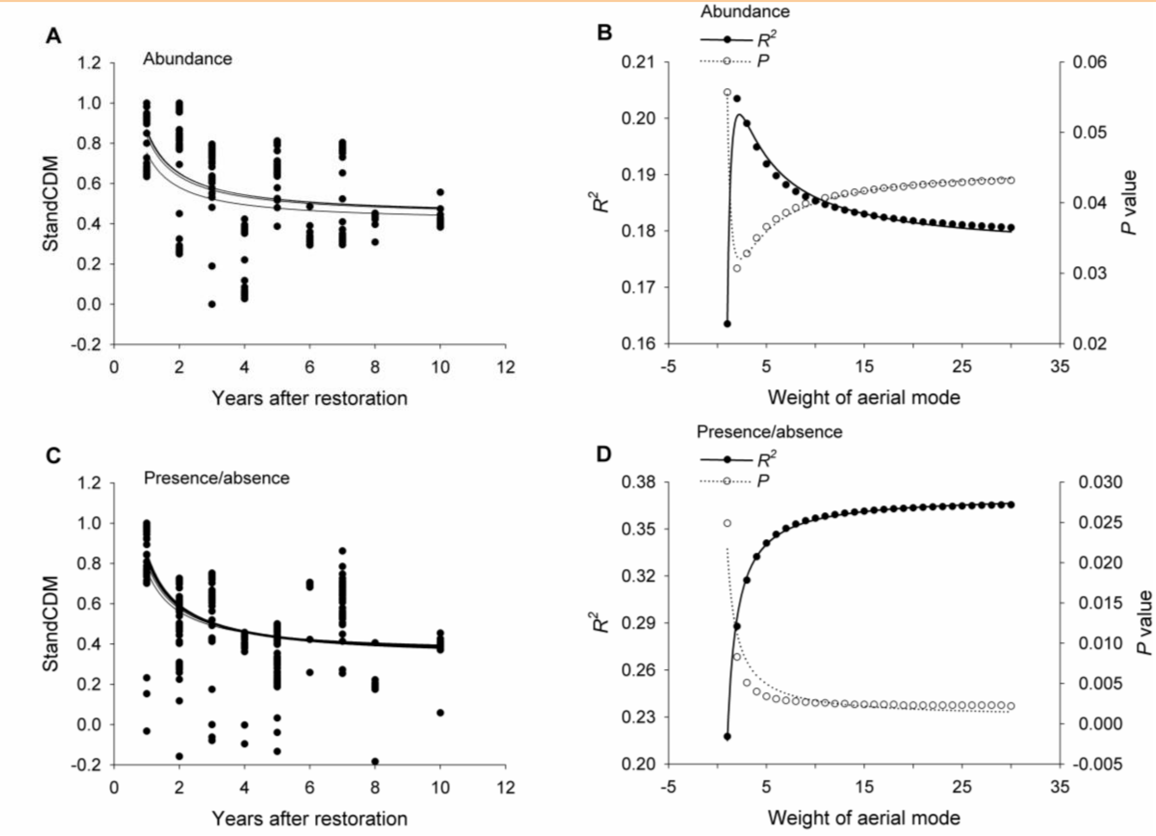
A
Abundance
StandCDM
1.2
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
0
2
4
6
8
10
12
Years after restoration
B
Abundance
R^2
P
0.21
0.20
0.19
0.18
0.17
0.16
0.06
0.05
0.04
0.03
0.02
-5
5
15
25
35
Weight of aerial mode
P value
C
Presence/absence
StandCDM
Years after restoration
D
Presence/absence
R^2
P
0.38
0.35
0.32
0.29
0.26
0.23
0.20
0.030
0.025
0.020
0.015
0.010
0.005
0.000
-0.005
Weight of aerial mode
P value

Fig. 2.

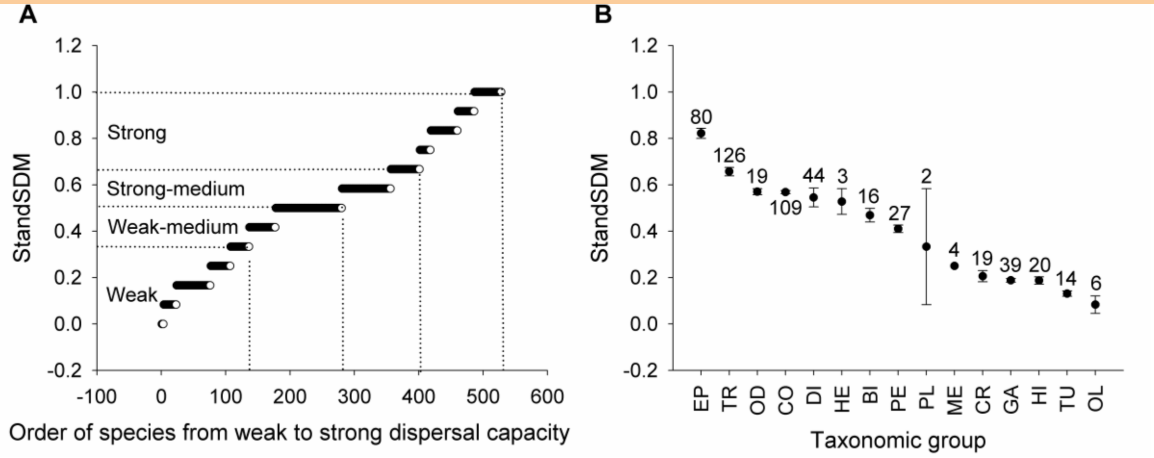
A
B
1.2
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
StandSDM
Strong
Strong-medium
Weak-medium
Weak
-100
0
100
200
300
400
500
600
Order of species from weak to strong dispersal capacity
80
126
19
109
44
3
16
27
2
4
19
39
20
14
6
EP
TR
OD
CO
DI
HE
BI
PE
PL
ME
CR
GA
HI
TU
OL
Taxonomic group

Fig. 3.

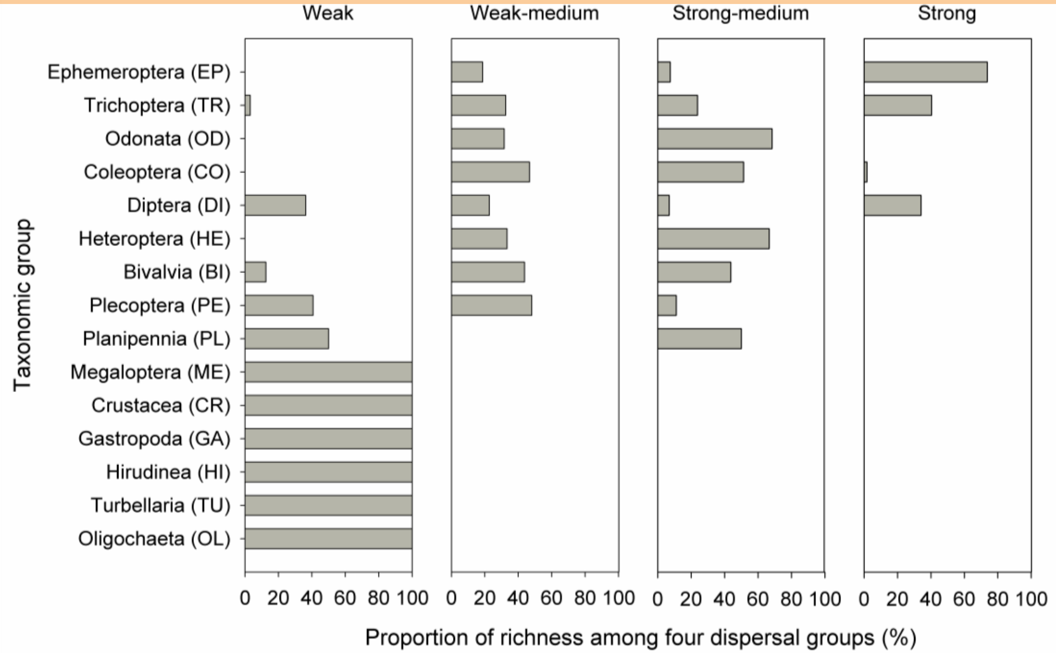
Weak
Weak-medium
Strong-medium
Strong
Taxonomic group
Ephemeroptera (EP)
Trichoptera (TR)
Odonata (OD)
Coleoptera (CO)
Diptera (DI)
Heteroptera (HE)
Bivalvia (BI)
Plecoptera (PE)
Planipennia (PL)
Megaloptera (ME)
Crustacea (CR)
Gastropoda (GA)
Hirudinea (HI)
Turbellaria (TU)
Oligochaeta (OL)
0 20 40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

Fig. 4.

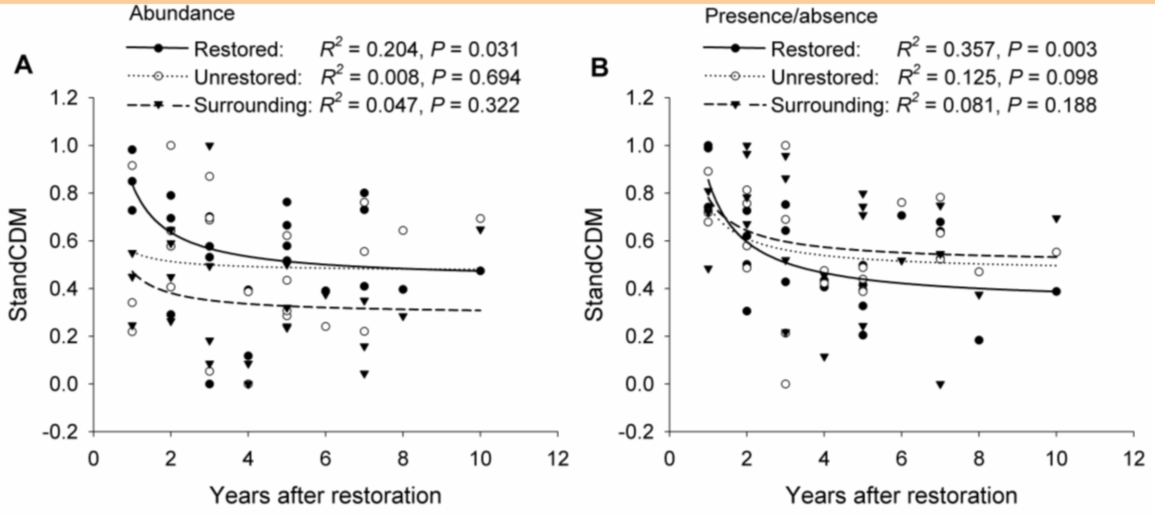
Abundance
A
Restored: R^2 = 0.204, P = 0.031
Unrestored: R^2 = 0.008, P = 0.694
Surrounding: R^2 = 0.047, P = 0.322
StandCDM
1.2
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
0
2
4
6
8
10
12
Years after restoration
Presence/absence
B
Restored: R^2 = 0.357, P = 0.003
Unrestored: R^2 = 0.125, P = 0.098
Surrounding: R^2 = 0.081, P = 0.188
StandCDM
Years after restoration

Fig. 5.

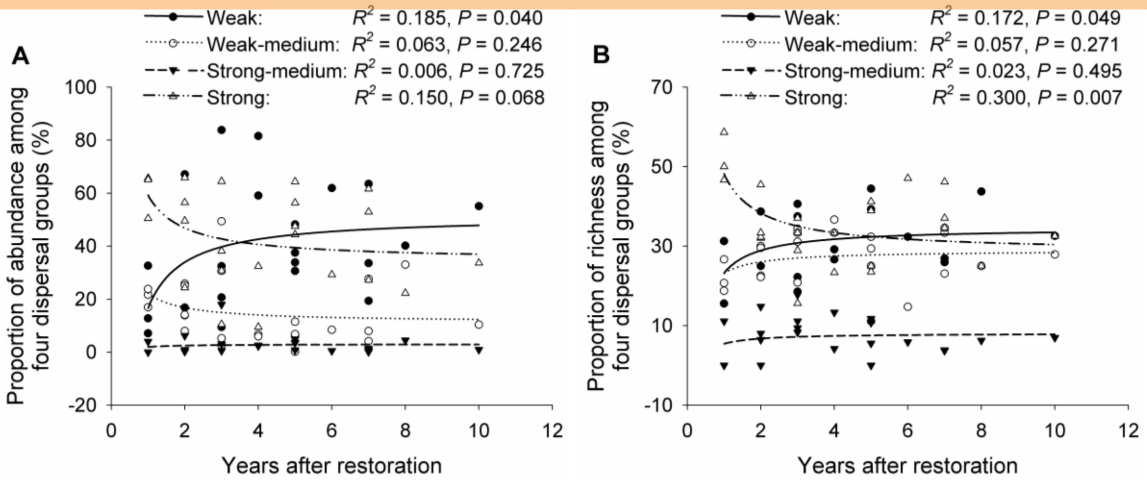
A
Weak: R^2 = 0.185, P = 0.040
Weak-medium: R^2 = 0.063, P = 0.246
Strong-medium: R^2 = 0.006, P = 0.725
Strong: R^2 = 0.150, P = 0.068
Proportion of abundance among four dispersal groups (%)
100
80
60
40
20
0
-20
0
2
4
6
8
10
12
Years after restoration
B
Weak: R^2 = 0.172, P = 0.049
Weak-medium: R^2 = 0.057, P = 0.271
Strong-medium: R^2 = 0.023, P = 0.495
Strong: R^2 = 0.300, P = 0.007
Proportion of richness among four dispersal groups (%)
70
50
30
10
-10
0
2
4
6
8
10
12
Years after restoration

Fig. 6.

Supplementary

Table S1. Values of the four dispersal modes and the standardized species dispersal metric (standSDM), 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 standSDM 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 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. 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 $P < 0.05$.

Variable	Weight	Entire community (Fig. 5)			Restored (Fig. 6 A, B)				Unrestored				Surrounding			
		Rest.	Cont.	Surr.	Q1	Q2	Q3	Q4	Q1	Q2	Q3	Q4	Q1	Q2	Q3	Q4
Abundance	1	0.164	0.018	0.060	0.001	0.136	0.009	0.229*	0.029	0.000	0.002	0.001	0.010	0.017	0.000	0.051
	2	0.204*	0.008	0.047	0.185*	0.063	0.006	0.150	0.000	0.015	0.001	0.005	0.042	0.022	0.000	0.040
	3	0.199*	0.005	0.042	0.155	0.025	0.000	0.150	0.000	0.031	0.030	0.005	0.045	0.034	0.003	0.040
	4	0.195*	0.004	0.039	0.155	0.024	0.000	0.150	0.000	0.031	0.030	0.005	0.045	0.034	0.003	0.040
	5	0.192*	0.004	0.038	0.155	0.024	0.000	0.150	0.000	0.031	0.030	0.005	0.045	0.034	0.003	0.040
	6	0.190*	0.004	0.037	0.155	0.024	0.000	0.150	0.000	0.031	0.030	0.005	0.045	0.034	0.003	0.040
	7	0.188*	0.003	0.036	0.155	0.024	0.000	0.150	0.000	0.031	0.030	0.005	0.045	0.034	0.003	0.040
	8	0.187*	0.003	0.036	0.155	0.024	0.000	0.150	0.000	0.031	0.030	0.005	0.045	0.034	0.003	0.040
	9	0.186*	0.003	0.035	0.155	0.024	0.000	0.150	0.000	0.031	0.030	0.005	0.045	0.034	0.003	0.040
	10	0.185*	0.003	0.035	0.155	0.024	0.000	0.150	0.000	0.031	0.030	0.005	0.045	0.034	0.003	0.040
	15	0.183*	0.003	0.034	0.155	0.024	0.000	0.150	0.000	0.031	0.030	0.005	0.045	0.034	0.003	0.040
	20	0.182*	0.003	0.034	0.155	0.024	0.000	0.150	0.000	0.031	0.030	0.005	0.045	0.034	0.003	0.040
	25	0.181*	0.003	0.033	0.155	0.024	0.000	0.150	0.000	0.031	0.030	0.005	0.045	0.034	0.003	0.040
	30	0.181*	0.003	0.033	0.155	0.024	0.000	0.150	0.000	0.031	0.030	0.005	0.045	0.034	0.003	0.040
Presence/	1	0.218*	0.084	0.049	0.184*	0.009	0.008	0.189*	0.082	0.041	0.000	0.028	0.004	0.007	0.004	0.033

absence	2	0.288**	0.106	0.069	0.263*	0.004	0.099	0.300**	0.161	0.082	0.044	0.013	0.059	0.074	0.024	0.046
	3	0.317**	0.114	0.074	0.189*	0.046	0.023	0.300**	0.112	0.029	0.063	0.013	0.058	0.045	0.002	0.046
	4	0.332**	0.118	0.077	0.172*	0.057	0.023	0.300**	0.112	0.029	0.063	0.013	0.055	0.042	0.002	0.046
	5	0.341**	0.120	0.078	0.172*	0.057	0.023	0.300**	0.112	0.029	0.063	0.013	0.055	0.042	0.002	0.046
	6	0.347**	0.122	0.079	0.172*	0.057	0.023	0.300**	0.112	0.029	0.063	0.013	0.055	0.042	0.002	0.046
	7	0.350**	0.123	0.080	0.172*	0.057	0.023	0.300**	0.112	0.029	0.063	0.013	0.055	0.042	0.002	0.046
	8	0.353**	0.124	0.080	0.172*	0.057	0.023	0.300**	0.112	0.029	0.063	0.013	0.055	0.042	0.002	0.046
	9	0.355**	0.124	0.081	0.172*	0.057	0.023	0.300**	0.112	0.029	0.063	0.013	0.055	0.042	0.002	0.046
	10	0.357**	0.125	0.081	0.172*	0.057	0.023	0.300**	0.112	0.029	0.063	0.013	0.055	0.042	0.002	0.046
	15	0.361**	0.126	0.082	0.172*	0.057	0.023	0.300**	0.112	0.029	0.063	0.013	0.055	0.042	0.002	0.046
	20	0.364**	0.115	0.082	0.172*	0.057	0.023	0.300**	0.112	0.029	0.063	0.013	0.055	0.042	0.002	0.046
	25	0.365**	0.114	0.082	0.172*	0.057	0.023	0.300**	0.112	0.029	0.063	0.013	0.055	0.042	0.002	0.046
	30	0.366**	0.127	0.082	0.172*	0.057	0.023	0.300**	0.112	0.029	0.063	0.013	0.055	0.042	0.002	0.046

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

Site	Code	Parameter			
		Years after restoration	Stream order	Elevation (m)	Catchment area (km^2)
Birkigsbach	A	5	4	120	25
Dill	B	2	6	217	314
Fallbach	C	4	2	127	30
Fauerbach	D	2	3	205	14
Fulda_Mecklar	E	2	7	196	2375
Fulda_Niederaula	F	2	6	207	1290
Gersprenz	G	1	6	162	154
Horloff	H	4	4	121	173
Josbach	I	5	3	268	29
Kinzig	J	7	6	134	885
Lache	K	3	3	104	11
Lahn	L	7	6	188	650
Nidda Bad Vilbel	M	6	6	96	1200
Nidda Ilbenstadt	N	1	6	104	1168
Nidda Ranstadt	O	3	5	129	226
Nidder	P	5	5	112	153
Niers	Q	7	5	26	658
Rodau	R	5	4	111	71
Ruhr	S	3	7	159	1000
Salz	T	3	5	144	83
Schwalm	U	10	4	28	250
Sulzbach	V	8	4	96	33
Ulster	W	1	5	242	384

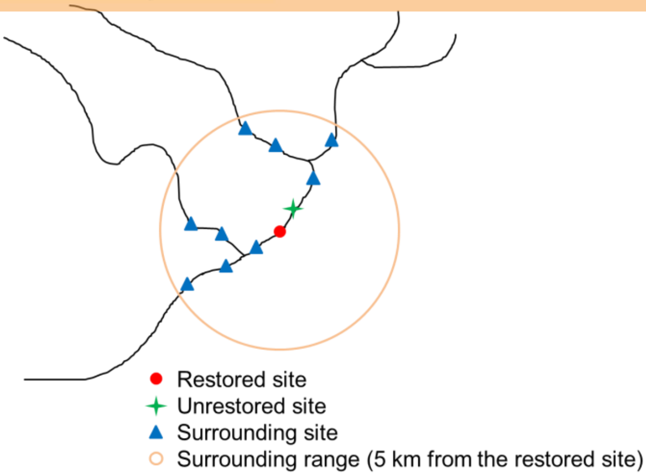

Fig. S1. Sketch map of the relative localities of the restored, unrestored, and surrounding sites.