# Colonisation patterns and -mechanisms of riverine benthic invertebrate communities following restoration of urban streams

*Besiedlungsmuster und -mechanismen von Makrozoobenthos Gemeinschaften in renaturierten Fließgewässern im urbanen Raum*

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# 1 Summary

## 1.1 English summary

Urban streams are severely impacted by anthropogenic pressures, resulting in reduced water quality and habitat diversity, which leads to a decline of benthic invertebrate diversity. Stream restoration aims to counteract this biodiversity decline by improving instream conditions and increasing habitat diversity, thereby creating new habitats for benthic invertebrates. However, benthic community recovery is often slow or absent. Reasons for this may be found in the mechanisms that control the recolonisation process: dispersal, tolerances (environmental filter) and biotic interactions (e.g., competition). According to the ‘Asymmetric Response Concept’ (ARC, Vos et al., 2023) their roles change predictably in space and time, but this has never been tested. To understand how dispersal, tolerances and competition interact during recolonisation, the three mechanisms need to be investigated in concert and their relative importance considered. Existing studies often lack detailed long-term data, leaving the patterns of recolonisation unresolved. This thesis addresses this research gap, using time-series data from the Boye catchment (Western Germany), which is characterised by urban land use and was used as open sewer for almost a century. The removal of wastewater, combined with hydromorphological restoration initiated a recolonisation process. This process and the underlying mechanisms were addressed in three chapters.

In the first chapter, ten years of monitoring data were analysed to identify general recolonisation patterns of benthic invertebrates and corresponding environmental drivers (Gillmann et al., 2023). Benthic communities became more similar and stabilised after eight years, with time since restoration being the main driver of community development. Habitat development, coupled with the increase in woody riparian cover, led to a shift in species assemblages. In the second chapter, the same time-series data was used to analyse the temporal changes of the communities’ traits, coupled to dispersal, tolerance and competition (Gillmann et al., 2024a). The communities’ dispersal capacity was highest directly after restoration and gradually decreased over time. Simultaneously, tolerance toward organic decomposition decreased, while tolerance toward chloride remained stable. On the other hand, interspecific competition (i.e., trait overlap) increased with time since restoration. In the last chapter, the role of the three filters was investigated based on 48 samples, collected in the Boye catchment in 2022. For the analysis, species- and site- specific data was used, including distance to source populations (dispersal filter), habitat suitability (environmental filter) and trait overlap (competition filter) (Gillmann et al., 2024b). Similar to chapter two, the dispersal filter was identified to be most important during initial recovery, while it continued to influence species distributions at more mature sites. The environmental filter significantly affected species distributions at sites unimpacted by historical sewage input and hydromorphological restoration. In contrast, a moderate effect was observed at ‘mature restored’ (> 10 years) sites, while no effect was observed at ‘recently restored’ (< 4 years) sites. Lastly, the competition filter was not a determining factor for species distributions, regardless of the restoration age.

The findings from this thesis are in line with the major assumption of the ARC that initial recovery depends on dispersal (Vos et al., 2023). Tolerances remain important if stressors are removed gradually. On the other hand, natural succession results in the increasing importance of environmental conditions over time. The competition filter showed contradicting results, indicating that trait overlap does not result in competitive exclusion.

In conclusion, this thesis provides valuable insights into the patterns and mechanisms acting during recolonisation of benthic invertebrates in urban streams. Despite the open sewer history of the Boye catchment, the communities recovered, following comparable patterns over time. This emphasizes that stream restoration efforts should continue to be directed at urban streams. These should consider the recovery trajectory of the ARC to remove possible barriers to recolonisation.

## 1.2 German summary

Flüsse im urbanen Raum sind stark durch menschliche Einflüsse geprägt, was zu einer verminderten Wasserqualität und dem Verlust von Lebensräumen führt. Daraus resultiert der Rückgang der Diversität von benthischen Zönosen. Um dem Verlust der Biodiversität entgegenzuwirken, werden immer mehr Flüsse renaturiert, wobei die Wasserqualität verbessert und neue Lebensräume für benthische Invertebraten geschaffen werden. Die Erholung der benthischen Zönosen verläuft jedoch oft langsam oder bleibt aus. Gründe dafür können in den Mechanismen liegen, die den Wiederbesiedlungsprozess steuern. Dazu gehören die Dispersion, Toleranz gegenüber Umweltstressoren (Umweltfilter) und biotische Interaktionen (z.B. Konkurrenz). Laut dem „Asymmetric Response Concept“ (ARC, Vos et al., 2023) variiert der Einfluss dieser drei Mechanismen im Laufe der Zeit. Diese Hypothese wurde jedoch nie getestet. Um zu verstehen, wie Dispersion, Toleranz und Konkurrenz während der Wiederbesiedlung interagieren, müssen diese drei Filter gemeinsam betrachtet und ihre relative Bedeutung untersucht werden. Dazu bedarf es detaillierter Langzeitdaten, die jedoch selten vorhanden sind. In dieser Arbeit wird diese Wissenslücke mithilfe von Zeitreihendaten aus dem Boye-Einzugsgebiet bearbeitet, das durch urbane Landnutzung geprägt ist und fast ein Jahrhundert lang als offener Abwasserkanal genutzt wurde. Die Entfernung des Abwassers, kombiniert mit der hydromorphologischen Renaturierung, initiierte einen Wiederbesiedlungsprozess. Dieser Prozess und die zugrunde liegenden Mechanismen wurden in drei Kapiteln behandelt.

Im ersten Kapitel wurden Monitoring-Daten aus zehn Jahren analysiert, um allgemeine Muster in der Wiederbesiedlung von benthischen Invertebraten und den zugehörigen Umweltfaktoren zu identifizieren (Gillmann et al., 2023). Die benthischen Zönosen wurden mit der Zeit ähnlicher und stabilisierten sich nach acht Jahren. Die Zeit seit Renaturierung war der Haupttreiber dieser Entwicklung. Durch die Zunahme der Ufervegetation, entwickelten sich komplexere Habitate, was zu Veränderungen in der Artenzusammensetzung führte. Im zweiten Kapitel wurden dieselben Zeitreihendaten verwendet, um die zeitlichen Veränderungen der Präferenzen in Bezug auf Dispersion, Toleranz und Konkurrenz innerhalb der Zönosen zu analysieren (Gillmann et al., 2024a). Unmittelbar nach der Renaturierung war die Zönose von einer hohen Dispersionskapazität geprägt, die über die Zeit abnahm. Die Toleranz gegenüber organischer Zersetzung nahm im Lauf der Zeit ab, während keine Veränderungen bezüglich der Chlorid-Toleranz festgestellt wurden. Schließlich nahm die interspezifische Konkurrenz (Überlappung von Artpräferenzen) mit der Zeit seit der Renaturierung zu. Im letzten Kapitel wurde die Rolle der drei Filter anhand von 48 Probestellen untersucht, die 2022 im Boye -

Einzugsgebiet gesammelt wurden (Gillmann et al., 2024b). Die Analyse basierte auf arten- und standortspezifischen Daten: die Entfernung zu Quellpopulationen (Dispersionsfilter), die Habitat-Eignung (Umweltfilter) und Artpräferenzen (Konkurrenzfilter). Ähnlich wie im zweiten Kapitel wurde der Dispersionsfilter als der wichtigste Faktor während der frühen Erholungsphasen identifiziert. Er beeinflusste jedoch ebenfalls die benthischen Zönosen an Standorten, die bereits länger renaturiert sind (> 10 Jahre). An Standorten, die nicht durch historischen Abwassereinfluss und hydromorphologische Renaturierungen beeinträchtigt wurden, war der Umweltfilter maßgebend für eine erfolgreiche Besiedlung. Derweil wurden geringe Auswirkungen für länger renaturierte bzw. keine Auswirkungen für frisch renaturierte Standorte beobachtet. Die interspezifische Konkurrenz war kein entscheidender Faktor für die Artenzusammensetzung, unabhängig vom Renaturierungsalter.

Die beschriebenen Ergebnisse stimmen größtenteils mit den Vorhersagen des ARC überein, wonach die Dispersion besonders in frühen Erholungsphasen wichtig ist und die Bedeutung der Umweltbedingungen über die Zeit zunimmt (Vos et al., 2023). Wenn Stressoren nur allmählich entfernt werden, spielen auch Toleranzen weiterhin eine Rolle. Dahingegen zeigten sich in Bezug auf die Konkurrenz widersprüchliche Ergebnisse, die darauf hinweisen, dass eine Überlappung der Präferenzen nicht zur Verdrängung von Arten führt.

Diese Arbeit liefert wichtige Einblicke in die Muster und Mechanismen, die während der Wiederbesiedlung von benthischen Invertebraten in urbanen Flüssen wirken. Trotz der ehemaligen Nutzung des Boye-Einzugsgebiets als offener Abwasserkanal, erholten sich die Zönosen im Laufe der Zeit, wobei sie ähnlichen Mustern folgten. Das zeigt, dass Renaturierungsmaßnahmen auch in Zukunft in urbanen Flüssen durchgeführt werden sollten. Dabei sollten die Muster des ARC berücksichtigt werden, um mögliche Barrieren für die Wiederbesiedlung zu entfernen.

# 2 General Introduction

## 2.1 The role of river ecosystems

Riverine ecosystems are among the most important ecosystems on earth (Jackson et al., 2001). They provide essential habitats for a diverse range of fauna and deliver numerous ecosystem services that benefit human societies (Everard and Powell, 2002; Dudgeon et al., 2006). These services encompass water supply, water quality control, microclimate regulation, tourism and recreation, erosion prevention and food supply (Hanna et al., 2018). In addition, they provide water for agricultural and industrial activities (Vári et al., 2022).

Despite their importance, streams worldwide are increasingly threatened, experiencing dramatic losses of biodiversity and habitat degradation caused by natural and anthropogenic stressors (Alcamo et al., 2008; Birk et al., 2020). Natural stressors to streams include extreme weather events such as heatwaves and high precipitation, which result in droughts and floods, respectively, and are predicted to become more frequent due to climate change (Domisch et al., 2013; Tabari, 2020; Chiang et al., 2021). In addition, anthropogenic pressures from expanding agricultural and urban activities threaten streams (Jones, 2001; Dudgeon, 2019) by introducing pollutants, destroying habitats, and altering natural flow patterns (Brooker, 1985; Horsák et al., 2009; Zerega et al., 2021; Schürings et al., 2022).

## 2.2 Anthropogenic impacts on urban streams

The impacts of human activities are especially apparent in streams in urban areas (further on called ‘urban streams’) which are the primary focus of this thesis. Walsh et al. (2005) described these streams to exhibit ‘urban stream syndrome’ due to the high population density surrounding them. Accordingly, urban streams are impacted by a combination of point and nonpoint source pollution (Neumann et al., 2002; Moore et al., 2017), hydrological changes (Baumgartner and Robinson, 2017) and hydromorphological alterations (Haase et al., 2013; Zerega et al., 2021). Discharge from factories or wastewater treatment plants (point source pollution), along with enhanced surface runoff (nonpoint source pollution) caused by impervious surfaces (Karlsen et al., 2019; Nguyen et al., 2023), introduces a variety of contaminates into streams. These contaminates include nutrients, ions, metals and pesticides, which can severely impair water quality (Paul and Meyer, 2001; Walsh et al., 2005; Burdon et al., 2016; Dittmer et al., 2020). For example, enhanced concentrations of chloride and other ions from wastewater and runoff can result in elevated conductivity (Koryak et al., 2001; Morgan et al., 2007; Barałkiewicz et al., 2014; Dittmer et al., 2020). Enhanced surface runoff additionally increases peak flows, causing erosion, and prevents precipitation from entering the ground. This reduction in groundwater recharge lowers the baseflow and increases the likelihood of desiccation in summer (Hancock, 2002; Ryan et al., 2010). On the other hand, wastewater treatment plant effluents can increase the baseflow of urban streams, maintaining flow during heatwaves and preventing desiccation (Bhaskar et al., 2016). Major hydromorphological changes include channelisation and the insertion of concrete riverbeds, which further increases flow velocity and reduces erosion, respectively (Booth et al., 2016; Auel et al., 2017). In addition, woody riparian vegetation is often removed, which increases stream temperature and evaporation rates, further enhancing the probability of desiccation (Kail et al., 2021). The accumulation of the stressors described, results in heavy degradation of urban streams, their habitats and their biotic communities, posing a special challenge for stream management and conservation (Walsh et al., 2005; Rumschlag et al., 2023).

## 2.3 Stream restoration challenges

The degradation of stream ecosystems has led to severe biodiversity decline (Birk et al., 2020). To counteract further degradation, the European Water Framework Directive (WFD; 2000/60/CE) was introduced in 2000, with the central aim for all European water bodies (ground and surface waters) to reach at least a good ecological status by 2027. The ecological status, defined in the WFD, is a measure of stream health which entails biological, physicochemical and hydromorphological parameters (European Union, 2008). Accordingly, these parameters were implemented in monitoring programs, to evaluate the ecological status of streams (Arle et al., 2016). Biological parameters provide the most comprehensive assessment of stream health, as the distribution and density of stream biota are influenced by stressors over longer timeframes, while physicochemical parameters only reflect current conditions (Barbour et al., 2000). Aquatic groups used for bioassessment include phytoplankton, macrophytes, phytobenthos, fish fauna and benthic invertebrates (Resh, 2008; Kenney et al., 2009; Haase et al., 2013). While all these groups have their advantages for bioassessment, benthic invertebrates are most frequently used (Hering et al., 2004; Masouras et al., 2021). They play an important role in stream ecosystems, as they serve many ecological functions, such as decomposition and nutrient cycling, and are an important part of the aquatic food web, acting as consumers and prey (Wallace and Webster, 1996). Further, they are abundant in stream ecosystems, vary in their sensitivity toward stressors and exhibit a range of ecological preferences (Kenney et al., 2009; Tampo et al., 2021).

To improve the ecological status of streams, the EU member states implemented different stream restoration measures. Major components of stream restoration efforts include dam removal to restore longitudinal connectivity (Magilligan et al., 2016), the removal of point source pollution to improve water quality (Thompson et al., 2018), hydromorphological restoration, such as the removal of concrete beds or addition of habitat structure to increase flow diversity (Quinn et al., 2009; Januschke et al., 2014; Verdonschot et al., 2016; Omoniyi et al., 2022) and the planting of woody riparian vegetation (Thompson and Parkinson, 2011). Woody riparian vegetation can significantly enhance the habitat quality of streams (Palt et al., 2023). Next to decreasing stream temperatures via shading (Davies-Colley et al., 2009; Kail et al., 2021), it stabilises streambanks and provides particulate organic matter and deadwood to the stream, which serve as important food source and shelter for various benthic invertebrate species (Purcell et al., 2002; Miller et al., 2010; Thompson and Parkinson, 2011; Kail et al., 2015).

After the streams conditions have been improved, the benthic communities were expected to quickly recolonise the restored habitats (‘Field of dreams’ hypothesis, Palmer et al., 1997). However, many studies have reported only minor responses of the benthic invertebrate community (Jähnig et al., 2010; Louhi et al., 2011; Violin et al., 2011; Leps et al., 2016; Al-Zankana et al., 2020). Positive effects have also been reported, but less frequently (England et al., 2021; Lorenz, 2021). Missing community responses often result from the failure of restoration measures to enhance the physical and hydrological conditions (Bond and Lake, 2003; Palmer et al., 2010; Brettschneider et al., 2023). In some cases, stressors acting on catchment scale, such as upstream point source pollution, continue to impair water quality, preventing the benthic invertebrate community to recover (Wolfram et al., 2021; Omoniyi et al., 2022; Verdonschot and Verdonschot, 2023). Habitat fragmentation and the absence of source populations may act as dispersal barriers and impede recolonisation of benthic invertebrate species (Sundermann et al., 2011; Tonkin et al., 2018). Additionally, the presence of a tolerant pre-restoration community can prevent the arrival of new species (‘negative resistance’, Wolff et al., 2019; Barrett et al., 2021). Lastly, initial recovery of communities following decades of water quality improvements can be delayed or reversed by the introduction of new stressors, e.g., pollutants, climate change and arrival of invasive species (Haase et al., 2023).

## 2.4 Patterns and mechanisms of benthic invertebrate recovery

Benthic invertebrate community recovery after stream restoration is strongly linked to the underlying mechanisms of recolonisation processes. The main drivers of recolonisation are summarised as spatial, environmental and biotic interaction filters, which are expected to act on the existing species pool in hierarchal order (Lake et al., 2007; Westveer et al., 2018). These drivers are similar to the ones described in metacommunity theory (Leibold et al., 2004; Lake et al., 2007; Heino et al., 2015), governing processes of community assembly. The spatial filter includes the species-specific dispersal capacities, the distance to source populations and other barriers to dispersal (Sundermann et al., 2011; Tonkin et al., 2018; Li et al., 2019). Dispersal plays an important role in the life-cycle of benthic invertebrates. Hololimnic species have aquatic larval and adult stages and are therefore mostly restricted to aquatic dispersal (Tonkin et al., 2018). However, aerial dispersal is also possible through vectors, e.g., via phoresy (Figuerola and Green, 2002; Alonso and Castro-Díez, 2008). Merolimnic species, on the other hand, have a flying adult stage and leave the water column for mating, allowing them to actively disperse through air and over long distances (Tonkin et al., 2014). Hence, benthic invertebrates can disperse along the river network or overland (Tonkin et al., 2018). Different indices were developed to quantify dispersal capacity, using dispersal traits collected in several databases (Schmidt-Kloiber and Hering, 2015; Li et al., 2016; Sarremejane et al., 2020). Active dispersal compensates for passive downstream drift (Kopp et al., 2001) and is necessary to recolonise habitats after disturbances from droughts or after stream restoration (Sarremejane et al., 2017). Rapid recolonisation of restored stream reaches was identified to be linked to the presence of nearby source populations and good connectivity, rather than being dependant on specific dispersal traits (Langford et al., 2009; Sundermann et al., 2011; Brown et al., 2018; Westveer et al., 2018). But pioneer communities were shown to consist of strong dispersing species (Winking et al., 2014; Lorenz, 2021).

The environmental filter describes the local conditions of a stream reach (Lake et al., 2007). Only species that perform well in a given habitat can occur, a process known as ‘species sorting’ (Leibold et al., 2004; Heino et al., 2015). Different species exhibit different preferences toward environmental conditions. The range of conditions that are potentially suitable for the species define their ‘fundamental niche’ (Hutchinson, 1957). This niche is narrow for sensitive species and wide for tolerant species (Heino and de Mendoza, 2016). Recolonisation success therefore depends on the fit between environmental conditions and the preferences of potential colonisers (Verdonschot et al., 2016). Local differences in water quality were found to determine community composition (Robinson et al., 2014). Consequently, sensitive species are more severely impacted by short-term disturbances due to natural or human-induced stressors that alter the streams conditions (Townsend, 1989). Environmental species sorting is expected to be closely linked to species dispersal (Smith et al., 2015; Csercsa et al., 2019). Good dispersing species can easily detect suitable habitats and establish at new sites (Pander et al., 2016). Species, not thriving in the given conditions, may still be able to persist, due to continuous influx from upstream as a result from high dispersal rates ('mass effects', Leibold et al., 2004; Sarremejane et al., 2017). The neutral theory of Leibold et al. (2004) suggests that differences in the community structure between different stream reaches are the result from random dispersal and environmental variability.

The 'realized niche' of a species describes the conditions where the species actually occurs (Hutchinson, 1957). This differs from the 'fundamental niche' due to biotic interactions that control local community dynamics (Lake et al., 2007). Interspecific biotic interactions involve trophic interactions or competition for food and space (Wisz et al., 2013). The degree of competition depends on the availability of these resources. Species that rely on similar resources are expected to compete with each other. Consequently, competition increases, if the essential resources are depleted (Barrett et al., 2021). Resource depletion and niche alteration, can prevent desired species from settling at the restored site, which is referred to as 'negative resistance and resilience' (Lake, 2013). Therefore, the order of arrival is relevant for the recolonisation success of benthic invertebrates, because early arriving species can prevent other species from settling due to priority effects (Little and Altermatt, 2018). This is especially problematic in the presence of a degraded pre-restoration community (Barrett et al., 2021). For example, mayflies were demonstrated to be outcompeted by large snail densities (White et al., 2021), while caddisflies were shown to be superior to mayflies and snails, if they arrived first (Eglesfield et al., 2023). In general, strong competitors are expected to outcompete weak competitors (Eglesfield et al., 2023), potentially leading to complete species replacement. However, such competitive exclusion was found to be a slow process, occurring over many decades to millennia (Yackulic, 2017). In stable communities, an equilibrium between local extinction and colonisation dynamics can influence local dynamics ('patch dynamics', Leibold et al., 2004).

In close relation to metacommunity theory, the Asymmetric Response Concept (ARC, Vos et al., 2023) offers a framework to predict community responses under varying stressor intensities. It suggests that the role of the three filters (dispersal, tolerances and biotic interactions) for community assembly varies predictably over temporal and spatial gradients of recovering streams (Figure 1). In degraded streams, the species-specific tolerances determine their occurrence, while the other two filters are less important. The species' dispersal capacity is important for rapid recovery post-restoration and biotic interactions mainly act on the newly established community. However, recovery may only be partial and communities can persist in degraded states, due to remaining stressors, barriers to recolonisation or reintroduction resistance (Vos et al., 2023).

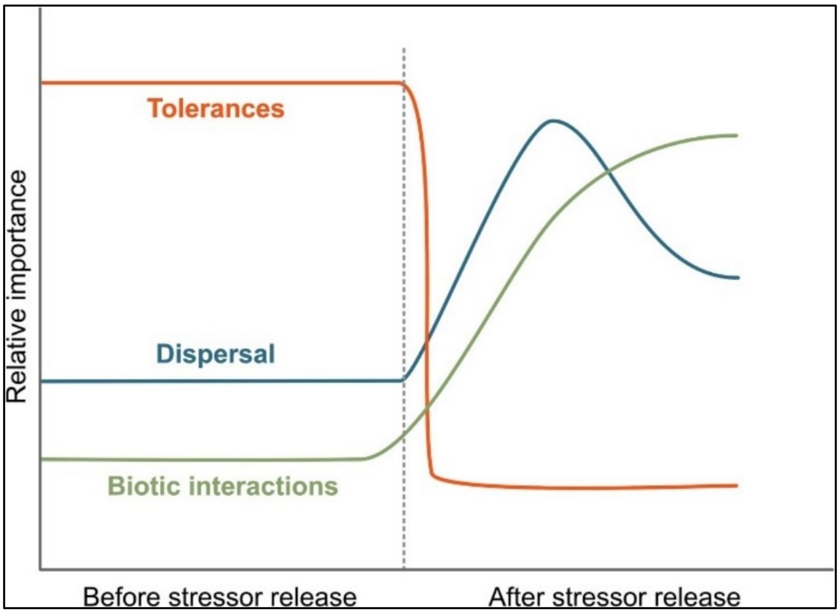


Figure 1: Conceptual figure, showing the main hypothesis of the Asymmetric Response Concept (ARC, Vos et al., 2023).

## 2.5 The importance of long-term studies

Understanding recolonisation patterns and their underlying mechanisms is crucial for restoration ecology. The ARC and metacommunity theories suggest that these are driven by the combined effect of three key factors, dispersal, environmental filtering and biotic interactions. While each of these factors has been investigated individually (section 2.4), some have been investigated in pairs (Csercsa et al., 2019). Schuwirth et al. (2016) created a model to disentangle the effects of biotic interactions and environmental factors on predicted community compositions. In addition, Shipley et al. (2022) integrated dispersal into traditional species distribution models to make individual predictions for dispersal-limited and non-dispersal limited species. However, testing the influence of the combined effect of the three factors during recolonisation patterns in the field is crucial to understand the effects of stream restoration on benthic invertebrates. Despite this, studies combining all three factors are lacking. Studying recolonisation patterns requires the observation of successional community development following restoration. Unfortunately, the assessment of restoration success is often only based on a space for time approach, e.g., comparing restored to natural and/or degraded sites, with the main goal of finding an increase in biodiversity in the restored site or at least a convergence of the reference and the restored sites (Winking et al., 2016; Lin et al., 2022). Spatial differences are only ‘snapshots’ of the current streams conditions and fail to demonstrate temporal patterns within the communities. Other studies only record short-term recovery, within one year after stream restoration (Winking et al., 2016; Baho et al., 2021). For example, Baho et al. (2021) found former culverts to be rapidly colonised by benthic invertebrates 9 month after they were opened up. Restoration success was recorded for up to five consecutive years (e.g., Friberg et al., 1998; Louhi et al., 2011). However, community composition recovery is a slow process and can take more than a decade (Lorenz, 2021). Hence, while short-term studies inform us about the composition of pioneer communities, they disregard the continuous habitat development and maturation of established communities (Winking et al., 2016; Baho et al., 2021; de Donnová et al., 2022) and the potential time lag caused by negative resistance and resilience (Barrett et al., 2021). Long-term studies incorporating large temporal gaps between samplings are also problematic (e.g., Muotka et al., 2002), because short-term effects from floods or droughts cannot be disentangled from the restoration effect. The investigation of more extensive and consecutive long-term data is therefore crucial to unravel the complex drivers of community recovery.

## 2.6 Aim of this thesis

The recovery process of benthic invertebrate communities is expected to follow a predictable pattern after stream restoration. Benthic invertebrate recovery is driven by a complex interplay of dispersal, as well as environmental and biotic interaction filters. A better understanding of these processes is necessary to explain limited biotic responses following stream restoration efforts. This requires detailed spatial and temporal data. The initial recolonisation of the Boye catchment was analysed by Winking et al. (2014, 2016). Since then, the same sites were sampled annually for their benthic invertebrate community. With the help of the time-series data collected in the Boye catchment, this thesis aimed to investigate recolonisation patterns of benthic invertebrates, with special emphasis on concepts predicted in the ARC, regarding the role of dispersal, environmental filtering and biotic interactions. More specifically this thesis aimed at:

(1) Investigating the changes in benthic invertebrate communities over time during the recovery in the previously nearly uninhabitable Boye catchment and identify the environmental drivers associated with these changes

(2) Analysing how community indices for dispersal capacity, tolerance and interspecific competition change during recovery from hydromorphological restoration

(3) Determining the roles of dispersal, environmental filtering and competition for community assembly during different phases of recovery from hydromorphological restoration

## 2.7 Characteristics of the Boye/ Emscher catchment

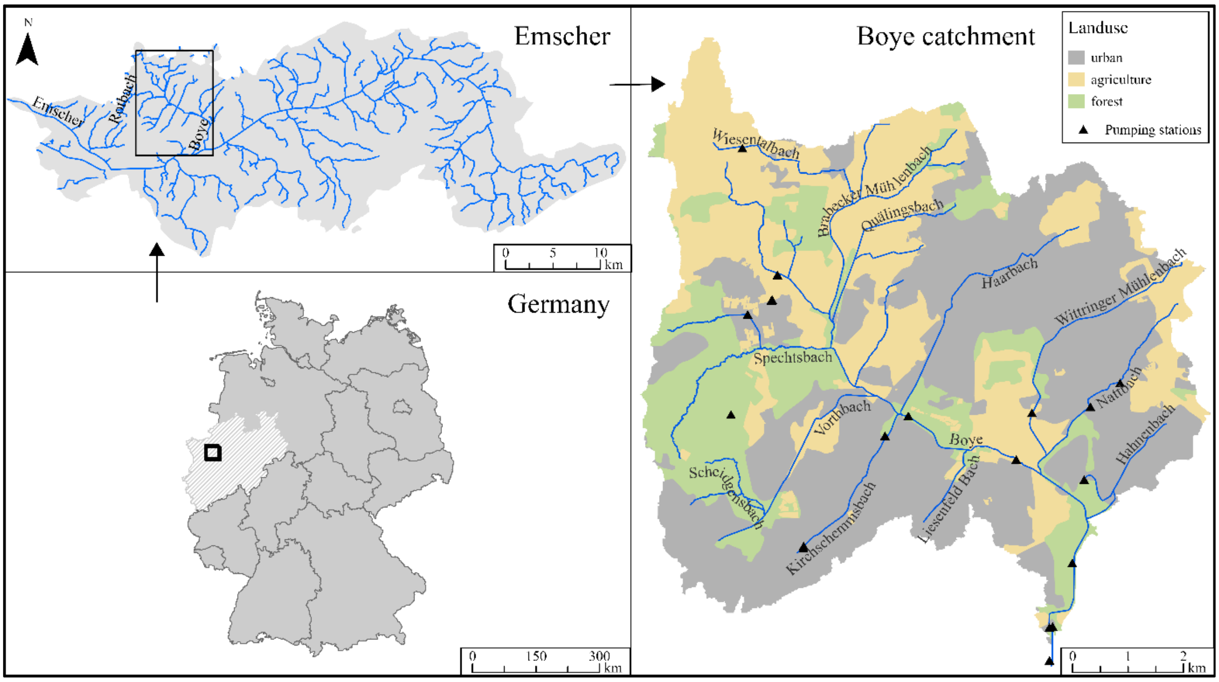


Figure 2: Map of the Boye catchment. Its location is marked on the Map of Germany (bottom left) and the Emscher catchment (top right). The map of the Boye catchment includes the major land uses (merged from CORINE and InVeKos), displayed in different colours: urban (grey), agriculture (yellow), forest (green). The pumping stations are displayed as black triangles (EGLV).

The strong habitat degradation of urban streams makes them an ideal testing ground to identify the effects of stream restoration and investigate the patterns of recolonisation. The analyses in this thesis focus on the Boye catchment which is located in the Ruhr Metropolitan Area of Western Germany, between Bottrop and Gladbeck (Figure 2). It is the second largest tributary of the larger Emscher catchment which flows into the river Rhine. The Boye catchment drains an area of 77 km², with its downstream section being dominated by urban infrastructure, while the upstream section is mainly influenced by agriculture and forest land use. All streams within the Boye system are characterised as sand dominated lowland streams (Type 14, Gellert et al., 2015). During industrialisation, the population density within the catchment increased and a solution was needed to transport sewage. Historic mining activities in the area resulted in land subsidence which made it impossible to build underground sewers. Consequently, the Boye and most of its tributaries were changed into open sewer channels with concrete beds, which transported sewage for almost a century. At the end of the 20th century, mining activities ended and an underground sewage system was built, marking the starting point of a large-scale restoration project which comprised the complete Emscher catchment (Gerner et al., 2018). The Boye catchment was gradually released from wastewater and restored, which mainly entailed the removal of the concrete beds and bank reinforcements. If possible, the streams were given more space to develop a meandering structure. The riparian vegetation was left to natural succession. However, the land subsidence that resulted from the mining history cannot be reversed and limits the extent of hydromorphological restoration measures. At one section of the Boye, this limit was overcome, by relocating the stream 1km to the north, before reconnecting it to the main stem. This allowed the restored stream section to develop more naturally (EGLV, 2019). Another problem of the land subsidence is that it is impossible for some stream sections to naturally connect to each other. Hence, pumping stations were installed at several locations in the catchment to either uplift the water, before pumping it into the next stream section, or to remove water from settlements and pump them into the underground sewage system (EGLV, 2021). Thus, despite the completion of morphological restoration of the Boye catchment in 2022 and the termination of wastewater input, it still suffers from hydrological alterations.

# 3 Published and submitted articles

The objectives of this thesis were thoroughly addressed in three separate articles. Two of which were published in peer-reviewed journals and one was published as a preprint:

**Chapter 1**: Gillmann, S.M., Hering, D. & Lorenz, A.W. (2023). Habitat development and species arrival drive succession of the benthic invertebrate community in restored urban streams. *Environmental Sciences Europe* 35, 49. https://doi.org/10.1186/s12302-023-00756-x

**Chapter 2:** Gillmann, S.M., Lorenz, A.W, Kaijser, W., Nguyen, H.H., Haase, P. & Hering, D. (2024a). How tolerances, competition and dispersal shape benthic invertebrate colonisation in restored urban streams. *Science of The Total Environment*, 929. https://doi.org/10.1016/j.scitotenv.2024.172665.

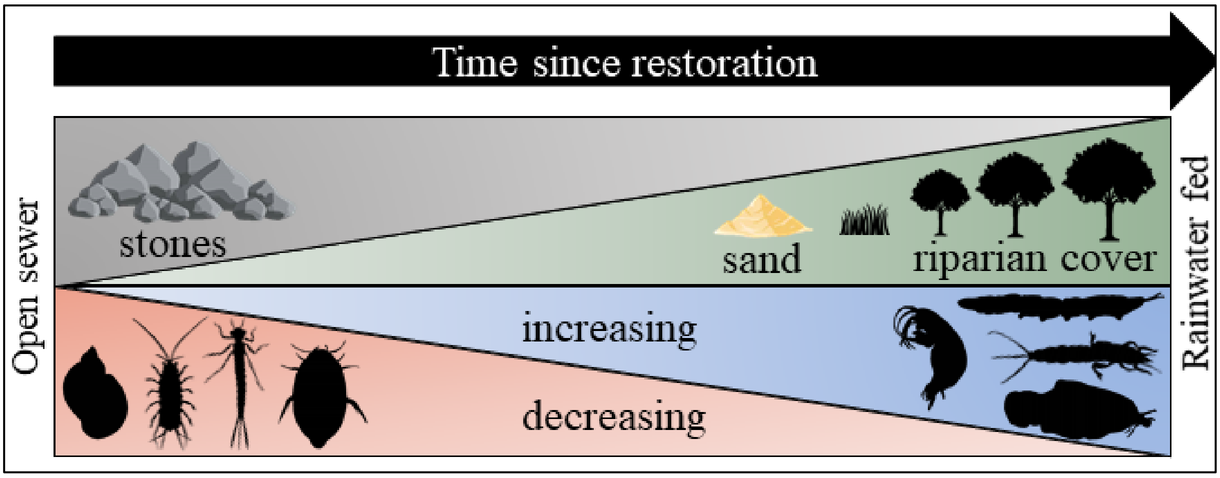
**Chapter 3:** Gillmann, S.M., Schuwirth, N., Lorenz, A.W. & Hering, D. (2024b). Contributions of source populations, habitat suitability and trait overlap to benthic invertebrate community assembly in restored urban streams (p. 2024.07.01.601525). *bioRxiv.* (preprint) https://doi.org/10.1101/2024.07.01.601525

The included articles, published in their respective journals' layout, have been provided with additional page numbers consistent with their positioning in the text of this thesis. A declaration of author contributions succeeds each article.

# Chapter 1

## Habitat development and species arrival drive succession of the benthic invertebrate community in restored urban streams

Published in *Environmental Sciences Europe* on 25th June 2023



Gillmann *et al. Environmental Sciences Europe* (2023) 35:49
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# Habitat development and species arrival drive succession of the benthic invertebrate community in restored urban streams

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**Abstract**

**Background** Urban streams are characterised by species-poor and frequently disturbed communities. The recovery of heavily polluted urban streams is challenging but the simple community structure makes recolonisation patterns more transparent. Therefore, they are generally applicable model systems for recolonisation of restored streams. Principal questions of stream restoration concern the drivers and patterns of recolonisation processes. Rarely, recolonisation of restored streams is recorded for a sufficient time to observe patterns of habitat and community development in detail. Over 10 years, we monitored benthic habitat changes and macroinvertebrate communities of eight restored sites in an urban stream network that was formerly used as an open sewer and thus, almost uninhabitable for macroinvertebrates prior to restoration. We analysed changes in environmental variables and communities with a selection of multi-variate analyses and identified indicator species in successional stages.

**Results** Proportions of stony substrate and conductivity decreased over time since restoration, while the riparian vegetation cover increased along with the amount of sandy substrate. The communities fluctuated strongly after restoration but began to stabilise after around eight years. TITAN analysis identified 9 species, (e.g. the mayfly *Cloeon dipterum* and the beetle *Agabus didymus*), whose abundances decreased with time since restoration, and 19 species with an increasing abundance trend (e.g. several Trichopteran species, which colonised once specific habitats developed). Woody riparian vegetation cover and related variables were identified as major driver for changes in species abundance. In the last phase of the observation period, a dry episode resulted in complete dewatering of some sites. These temporarily dried sections were recolonised much more rapidly compared to the recolonisation following restoration.

**Conclusions** Our results underline that community changes following urban stream restoration are closely linked to the evolving environmental conditions of restored streams, in particular habitat availability initialised by riparian vegetation. It takes about a decade for the development of a rich and stable community. Even in streams that were almost completely lacking benthic invertebrates before restoration, the establishment of a diverse macroinvertebrate community is possible, underlining the potential for habitat restoration in formerly heavily polluted urban areas.

**Keywords** Community composition, Habitat availability, Indicator species, Long-term monitoring, Stream recolonisation, Recovery ecology

## Background

Effects of stream and river restoration on riverine biota are often minor. This is particularly obvious for benthic macroinvertebrates that are strongly affected by anthropogenic stressors and are frequently used to monitor ecological status and restoration success [64]. Numerous studies document the poor response of

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macroinvertebrates to particularly hydromorphological restoration measures [13, 15, 19, 31, 64], but the reasons remain speculative. In many cases, restoration may have merely improved the hydromorphological conditions, while poor water quality remains to affect biota and prevents sensitive species from entering the system [12, 17, 43, 48]. Furthermore, low dispersal ability of the species, the distance to population sources and their connectivity to restored stream sections or the lack of source populations restrict recolonisation [6, 28, 57–60, 68, 71]. Finally, species that have established populations under degraded conditions may inhibit the recovery of sensitive species through competition [4, 37, 66, 73].

Consequently, the understanding of stream restoration effects is strongly linked to the understanding of recolonisation patterns and processes. In general, recolonisation starts once disturbances that deteriorated the original community have been lifted. Relevant disturbances of stream communities include natural events (such as floods and streambed drying) but in particular human-induced pollution and habitat modification [65, 67]. These anthropogenic pressures are especially common in urban streams, which are often channelised to fit the urban structure and are additionally impacted by stormwater runoff, and input from point or non-point sources [5]. Recolonisation after anthropogenic disturbances is often initialised by restoration measures, which amongst others aim to enhance the stream's biodiversity [44, 65]. Depending on the restoration goals different measures are implemented [55], including wastewater purification and a variety of hydromorphological measures, e.g. removal of bank reinforcements, revegetation of stream banks, and introduction of woody structures (deadwood) into the stream [10, 22–24, 62].

For a better understanding on how restoration initiates macroinvertebrate recolonisation, or fails to do this, the process needs to be broken down into its components. Recolonisation processes are guided by the habitats and environmental conditions provided by the restoration measures. In addition, it is impacted by the arrival of species that favour these conditions and by the occupation of niches of early establishing species, i.e. by competition patterns [66]. A direct result of most restoration measures is the presence of new, unoccupied habitats. Water quality improvement provides niches for species depending on high oxygen concentrations, while the removal of bank reinforcements results in more space for the stream, lower current velocities, and consequently the provision of habitats for lentic species [22]. More generally, restored streams develop more heterogeneous flow patterns, which ultimately leads to higher substrate diversity [45] providing niches for additional species. The establishment of woody riparian vegetation at the stream banks initialises natural succession [50, 62] and a change from open to shaded habitats, as the riparian areas mature. Woody riparian vegetation provides different functions to the stream as it increases the input of particulate organic matter and woody debris, which acts as an important food source and habitat for many benthic species, respectively. In addition, it provides shade, thus mitigates water temperatures and reduces primary production, which favours additional species and allows them to settle [10, 24, 39].

These frequently occurring effects of restoration support various threads of succession and recolonisation: From pollution-tolerant to pollution-sensitive species, from the community of a single habitat to communities of more variable habitats, and from communities of unshaded to those of shaded habitats. The new habitats that are created during restoration are quickly colonised by strong dispersers [30, 72]. This process largely depends on the species pool of the near surroundings and the species dispersal ability [53, 59, 60, 71]. The later arriving species, however, must compete for space and food with species already present, making it more difficult for new species to establish a population. Niches that are occupied at first will change during maturation but also following natural events such as floods and streambed drying [27, 35]. In conclusion, the macroinvertebrate community of restored streams is expected to undergo a distinct succession, driven by habitat availability, dispersal, and competition patterns.

However, this process can rarely be studied in the field and therefore remains hypothetical. Investigating patterns of recolonisation requires continuous long-term studies while existing studies merely focus on the first 1–5 years following restoration [14, 31, 69]. Often there are large temporal gaps between sampling, making it difficult to distinguish restoration effects on macroinvertebrate communities from natural variation unrelated to restoration [34, 36]. In addition, the existing studies on recolonisation patterns are impacted by the lack of information on the pre-restoration community, thereby limiting our ability to accurately interpret these patterns.

Here, we investigated an almost unique situation: The Boye stream network that has been completely restored and was used as an open sewer before restoration. The Boye exemplifies the challenges of restoring urban streams that go well beyond those stream restoration endeavours in rural areas: Strong pollution prior to restoration, limited space for habitat development, few recolonisation sources and multiple barriers for recolonising species [71]. The Boye is part of the Emscher catchment (Western Germany), which was for almost a century used as an open sewer channel for the urban hub Ruhr Metropolitan Area (>5 million people) until it was restored over the last 20 years. Therefore, only few very tolerant organisms were able to survive in the system. This strong degradation offers unique opportunities for disentangling recolonisation patterns: Due to the limited number of species in the system prior to restoration, the majority of available niches will be occupied by newly arriving species. Consequently, the succession of habitats following restoration conditions and the recolonisation with invertebrates following the development of habitats and dispersal processes can be observed without being "disturbed" by a diverse pre-restoration assemblage. An initial analysis of the development of the benthic invertebrate community in the Boye catchment was conducted by Winking et al. [71, 72] and the sampling of the community in a number of restored sites was continued yearly, over a period of 10 years.

Based on the successional processes described above, we hypothesize: (1) The inter-annual within and between site variability of the communities' species composition decreases with time since restoration. (2) After restoration, there will be a continuous development of habitats caused by gradual maturation of the sampling sites, which drives community development. (3) Many species that firstly colonised the restored stream reaches vanish quickly due to the ongoing changes in habitat availability, water quality and the arrival of new (competing) species. (4) Over time, the natural succession of riparian vegetation will lead to an increase in shade levels, thereby creating favourable habitat for the establishment of species that depend on such conditions. The species that increase in abundance over time are therefore positively associated with shade.

## Materials and methods

### Study area

The Boye catchment is located in the Ruhr Metropolitan Area in Western Germany. It is part of the Emscher catchment, which drains into the river Rhine. It has a size of 77 km$^2$ and a total stream length of 90 km (Fig. 1). The downstream parts of the catchment are situated in a highly urbanized area, while the upstream sections are mainly surrounded by agricultural land and forests. In the beginning of the twentieth century, the Emscher and large parts of its tributaries, including most of the Boye network, were transformed into concrete channels to transport domestic wastewater [71, 72]. Between 1993 and 2021 the aboveground streams were restored by building underground sewers to transport the wastewater. The concrete bed and bank reinforcements were removed, the streambeds widened and changed from straightened to sinuate or semi-meandering. Woody riparian vegetation developed naturally.

In spring 2012, several restored sites were selected for monitoring of benthic invertebrates, eight of which were used for our study (Table 1). We selected sites of a similar stream size (i.e. 1st to 2nd order streams) that were restored not more than 14 years ago. Compared to Winking et al. [71] we excluded two sites that were restored 19 years ago and were already in an advanced succession stage when the investigations started, and two sites in sections of larger streams (i.e. the main stem of the Boye thus 2nd to 3rd order streams), which community is hardly comparable. The selected sites differ in time since wastewater was removed and in time since hydromorphological restoration was conducted. Therefore, the first year and years 11 to 14 after restoration are only represented by two sites (Natt, Voun and Kirun, Kirob, respectively). All sites cover the period from 5 to 10 years after restoration. In accordance with our hypotheses, we related the occurrence of individual species and their change in abundance to different parameters: years since wastewater removal and hydromorphological restoration, water quality parameters, the proportion of different microhabitats and shade level.

### Sampling, sorting and identification

From 2012 to 2021, the eight sites (Table 1) were sampled yearly in March or April. At each site, standardised multi-habitat-sampling was performed [18] and the following water quality parameters were measured: pH, temperature (°C), conductivity (µS/cm), and oxygen (mg/l). The cover of microhabitat types was estimated in 5% steps and only microhabitats with more than 5% cover were included in the composite sample. Reflecting the estimated cover of microhabitats, 20 sampling units were taken using a hand net (25 × 25 cm, 500 µm mesh size). One sampling unit represented 5% of all present microhabitats. The samples were pooled and preserved in ethanol (96%). The pooled samples were sorted in the laboratory using a standardised subsampling procedure [33]. The specimens were identified according to the operational taxa list for Germany [18], if possible, to species level, except for Chironomidae (tribe level), Diptera (family level) and Oligochaeta (family level). Species counts were standardised to abundance (Ind/m$^2$). The resulting taxalist was adjusted prior to analysis, to account for varying identification levels of different larval instars [41].

### Shade level

For the determination of the shade level, percentage riparian cover was used as a proxy. Satellite images and orthophotos were analysed in ArcGIS (version 7.0) to identify the riparian cover in a 500 m long und 20 m wide upstream corridor of each sampling site according

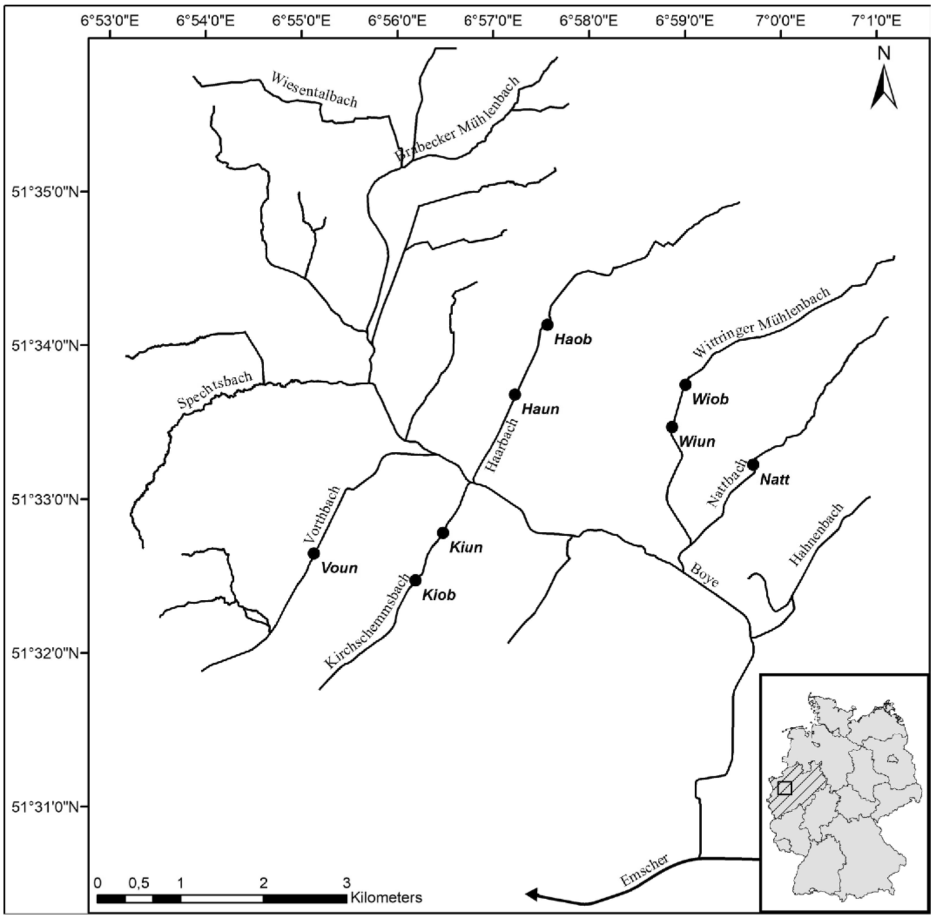

**Fig. 1** Map of sampling sites (black dots) in the Boye catchment (Ruhr Metropolitan Area, Western Germany)

**Table 1** List of the restored sampling sites within the Boye catchment

| Stream name | Site ID | Coordinates | Wastewater-free since | Hydromorphological restoration |
|---|---|---|---|---|
| Haarbach | Haun | 51.56279°N 6.956702°E | 2009 | 2010 |
| Haarbach | Haob | 51.570724°N 6.960792°E | 2009 | 2010 |
| Kirchschemmsbach | Kiun | 51.548051°N 6.943958°E | 2007 | 2007 |
| Kirchschemmsbach | Kiob | 51.541859°N 6.939128°E | 2007 | 2007 |
| Nattbach | Natt | 51.557192°N 6.999138°E | 2009 | 2011 |
| Vorthbach | Voun | 51.544019°N 6.921747°E | 2007 | 2011 |
| Wittringer Mühlenbach | Wiun | 51.560245°N 6.98305°E | 2009 | 2010 |
| Wittringer Mühlenbach | Wiob | 51.564035°N 6.986361°E | 2009 | 2010 |

to a modified procedure from Kail et al. [24]. Instead of the automated object-based image analysis, woody vegetation was marked manually. The proportions of shaded and unshaded areas within the aforementioned buffer were calculated in Rstudio (version 4.1.2). Satellite images of the Boye catchment were available from

Tim-Online (https://www.tim-online.nrw.de/tim-online2/, 9th Aug 2021) for every third year from 2012 to 2018. For 2020, orthophotos were available from ELWAS-WEB [29]. The percentage riparian cover of missing years was complemented with the moving average of the previous and next known values. Hereafter, the percentage riparian cover will be referred to as 'shade'.

### Data analysis

All statistical analyses were conducted using Rstudio v4.1.2 [51]. All figures were created with the package "ggplot2" (v3.3.5, [70]).

Hypothesis (1) (community variability decreases with time since restoration) was addressed by first calculating the number of taxa that occurred in every sampling site per year and plotting them as a function of the time since restoration (TsR [years]). Here, a generalized linear model (GLM) with Poisson error distribution and identity link function was used. The independent variable (TsR) was log transformed. Due to the different years in which the streams were restored, the first year after restoration is only represented by two sampling sites (sites Natt and Voun). From year 11 onward, data were only available from two other sampling sites: Kirun and Kirob.

The patterns of community assembly were investigated with non-metric multidimensional scaling (NMDS). This was based on the Bray–Curtis dissimilarity index and applied on log(x + 1) transformed community data. Differences between the assemblages of different years since restoration were tested with a permutational multivariate analysis of variance (perMANOVA). To investigate the variability of the assemblages within each stream over time, the Jaccard dissimilarities were compared as a function of TsR. A GLM with Beta error distribution and logit link function was fit to the data. Here, presence/absence data was used instead of abundances, because merely the change in species composition was of interest. For these analyses, the "vegan" package (v2.5–7, [42]) was applied.

The second hypothesis (habitat development after restoration and impact on community succession) was tested by analysing the relationship between explanatory variables and communities. The following variables were addressed: 1) water quality variables: conductivity [µS/cm], $O_2$ [%], pH; 2) coverage of substrates [%]: gravel/stones, sand/sludge, loam, particulate organic matter (POM, fine and coarse), macrophytes (emergent and submergent), living parts of terrestrial plants (LPTP), algae (according to the microhabitat distribution from the benthic invertebrate field protocol); 3) level of shade [%]; 4) time since wastewater removal (TsW [years]); 5) time since restoration (TsR [years]).

Correlations between environmental variables were checked on forehand with the "cor" function of the "stats" package (v4.1.2 [51]). The variable "time since wastewater removal" (TsW) was highly correlated ($r = 0.93$) with the TsR and was therefore excluded from further analysis. All other correlations were below 0.6, thus, no other variables were excluded (Additional file 1: Table S1).

The main gradients influencing the taxonomic composition were identified via redundancy analysis (RDA) (package "vegan", v2.5–7, [42]). Prior to analysis, the explanatory variables were scaled. The effect of the explanatory variables on changes in species abundance was tested with an analysis of variance (perMANOVA). The variables that best explained the changes in abundance were identified using the forward selection method ("ordiR2step" function, package "vegan", v2.5–7, [42]) of the RDA applied to log(x + 1) transformed community data.

To test the third hypothesis (early colonising species vanish with habitat succession), first the species most responsible for temporal community changes within and between the sampling sites were identified. We applied the TITAN analysis [2] that is included in the package "TITAN2" (v2.4.1, [3]). Time since restoration was used as a gradient to identify indicator species that show a negative (z-), i.e. decreasing, or positive (z +), i.e. increasing, trend over time. Before the analysis, taxa with less than three occurrences across all samples were excluded, resulting in 77 taxa. Only species with purity and reliability levels above 0.9 were considered as indicators. The value of 1000 replicates was chosen for bootstrap resampling. For the resulting indicator species, their frequency of occurrence across sampling sites per year since restoration was calculated.

Finally, to test the fourth hypothesis (impact of riparian vegetation), the relationship of the explanatory variables on the indicator species excluding TsR was identified via another forward selection of the RDA. The resulting variables were displayed together with the indicator species abundance gradients in a multi-factorial analysis (MFA), created within the package "Factoshiny" (v2.4, [63]).

## Results

### H1: Community variability decreases with time since restoration

Over the 10 years of sampling, 130 taxa were identified across all sampling sites. The number of taxa per sampling site increases over time. The greatest increase in taxa number was found four years after restoration (Fig. 2). The regression coefficient is significantly different from zero $p < 0.001$ (mean = 3.4, 2.5% = 1.8, 97.5% = 4.93).

The NMDS of the log-transformed community data shows that the communities change along a temporal gradient at all sites (Fig. 3) (stress = 0.167). The differences between communities of different times since restoration were confirmed by a perMANOVA ($F = 11.53$, $p < 0.05$). While the communities at sites sampled in the first years after restoration (2012–2014) are very dissimilar to each other, communities at sites sampled in 2021 are very similar. Thus, the communities move along the gradient of time since restoration, becoming more similar over time.

The generalised linear regression model shows that Jaccard dissimilarities between samples of a given sampling site decline with the time since restoration (Fig. 4). The regression coefficient is significantly different from zero $p < 0.001$ (mean = − 0.12, 2.5% = − 0.15, 97% = − 0.08). The dissimilarity between communities decreases with time. Within the first eight years, the dissimilarity decreases by 30–50% at some sites. The model explains 43% of the variance within the data. The summer 2018 was unusually dry, causing some of the study streams to dry out (Additional file 3: Table S1). The communities that were sampled following this dry period (2019–2021) are displayed in grey (Fig. 4). The outliers in the years 13 and 14 after restoration are part of these communities. After the dry period, the Jaccard dissimilarity increases at two sampling sites.

### *H2: Habitat development after restoration and impact on community succession*

The relationship between environmental variables and overall community variability was analysed, using a RDA on the log(x + 1) transformed community matrix (Fig. 5). The permutation test shows that the environmental variables included in the model have a significant effect on the community composition ($F = 2.8$, $p < 0.05$). Most of the variance is explained by the time since restoration (RDA1 = − 0.97), followed by conductivity (RDA1 = 0.47) and the percentage of shade (RDA1 = − 0.43). The correlation matrix reveals that none of the environmental parameters are highly correlated with each other ($r > 0.7$, Additional file 1: Table S1). The highest correlation coefficient is observed for the coverages of algae and loam ($r = 0.58$). All other correlation coefficients are below 0.5. The gradients in the RDA show that the proportion of sand and sludge and the percentage of shade increase with time since restoration, while the percentage of loam, algae, POM, as well as pH and conductivity decrease over time.

The forward selection of the RDA identified six explanatory variables to be most important for the changes in

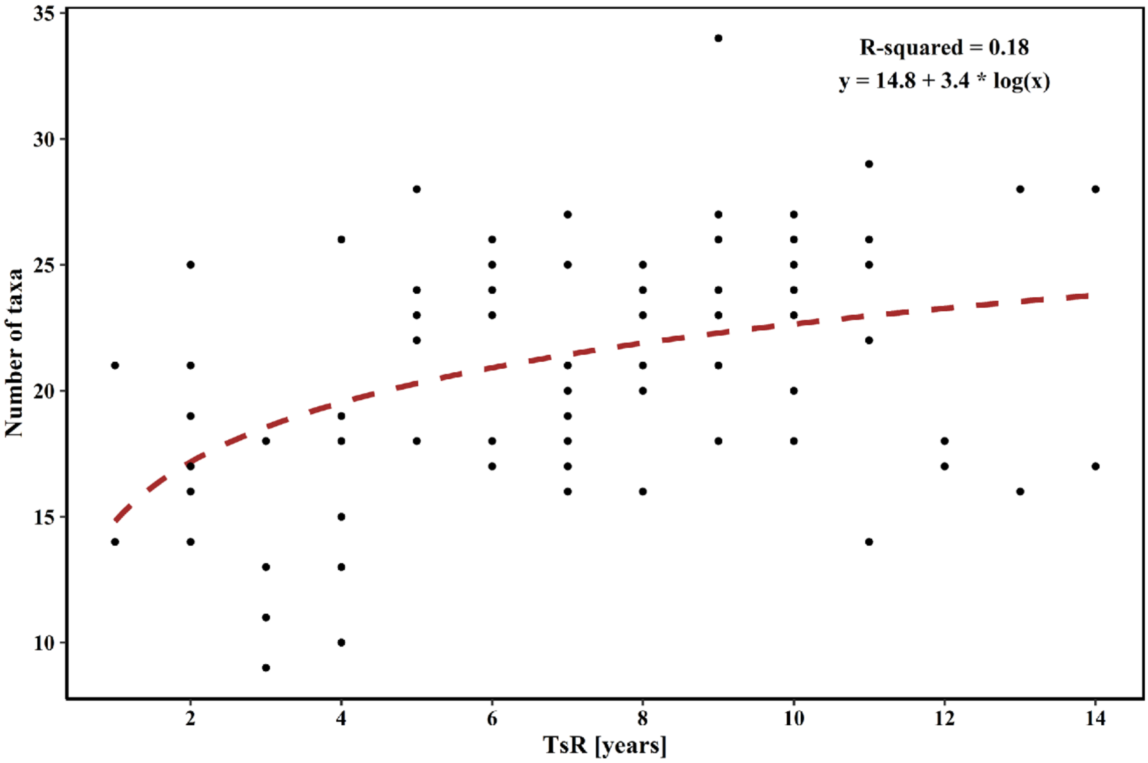

**Fig. 2** Generalised linear model (GLM) of the number of taxa per sampling site as a function of time since restoration (TsR). A Poisson error distribution and identity link function was used on the log transformed independent variable (TsR)

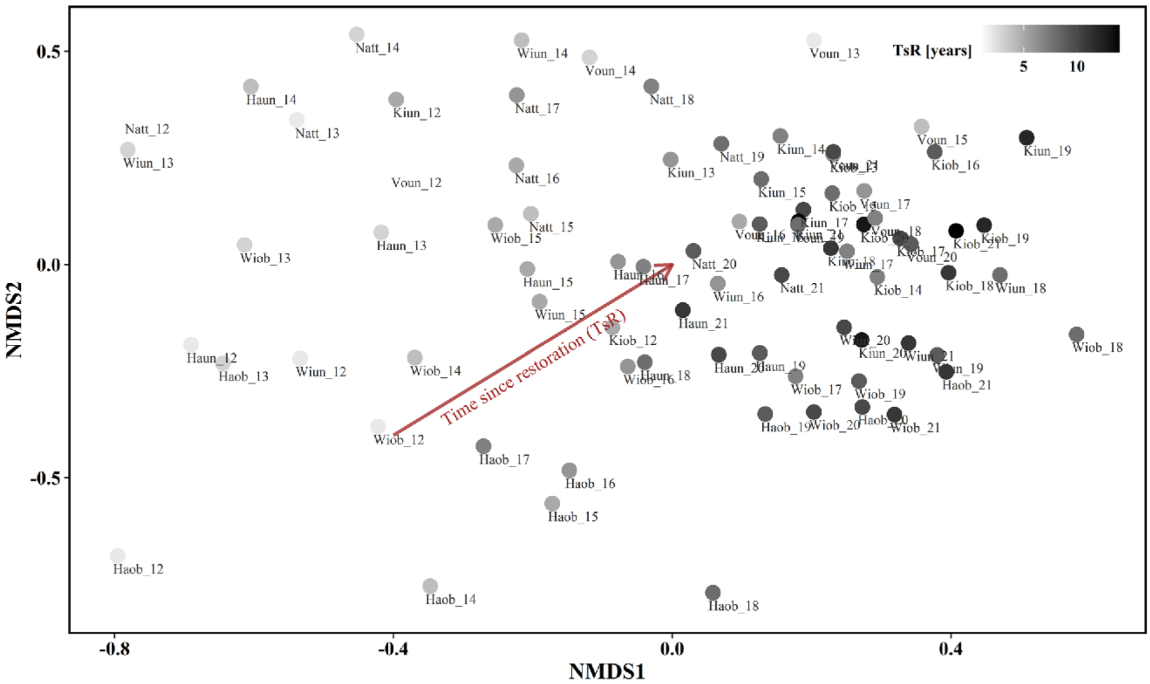

**Fig. 3** NMDS of log-transformed community data of eight restored sampling sites in the Boye catchment for 10 consecutive years (stress = 0.167). The points are coloured according to the time since restoration (TsR), measured in years. The numbers behind the sampling site Ids depict the sampling year (e.g. 12 = 2012). TsR was added as an overlay and is displayed by the arrow. Figures per sampling site are shown in Additional file 1: Figure S1

species abundances: TsR ($p = 0.002$), shade ($p = 0.002$), the proportion of gravel/stones ($p = 0.002$), sand/sludge ($p = 0.002$), POM ($p = 0.006$) and loam ($p = 0.022$) (Table 2).

For individual sampling sites, the community composition changes along different gradients (Additional file 2: Figure S2). For example, the community composition of the the Haarbach (Haun, Haob) moves along the gradient of gravel/stones. Conductivity and pH decrease with time since restoration. In the first years after restoration, conductivity is especially high in the Nattbach and Haarbach, while pH is high in the Vorthbach (Voun) and the up- and downstream sites of the Wittringer Mühlenbach (Wiob). The percentage of shade and the proportion of sand/sludge cover increase with time, in particular in the Wittringer Mühlenbach (Wiun, Wiob), the Haarbach (Haun) and the Vorthbach (Voun). The communities of the Kirchschemmsbach (Kiob, Kiun) mainly change along the temporal gradient of time since restoration.

The samples in streams that completely fell dry in the year 2018 are marked in red in Fig. 5. This was the case for three of the sampling sites (Natt, Voun and Wiob). Their communities appear to have moved a step backward along the gradient of time since restoration (TsR), compared to other sites, e.g. Haob.

### *H3: Early colonising species vanish with habitat succession*

The main species responsible for the temporal changes and therefore successional processes were identified using the TITAN analysis with time since restoration as a gradient. Nine species were identified, which abundance decreases with time since restoration (Fig. 6a). Five of these mainly occur immediately after restoration, four of which belong to the order of Coleopterans. However, the other species all belong to different taxonomic groups. *Cloeon dipterum* (cloedipt) for example is an Ephemeroptera and was only found the first two years following restoration. *Radix balthica* (radibalt), belonging to the class of Gastropoda, is always present, but its abundance decreases with succession, which is also true for the Trichoptera *Hydropsyche angustipennis angustipennis* (hydrangu).

In total, 19 species show an increasing abundance trend. Most of these species belong to the order of Diptera, as for example *Prodiamesa olivacea* (prodoliv) and *Eloeophila* sp. (eleosp). In addition, different Trichopterans, e.g. *Athripsodes bilineatus* (athrbili) and

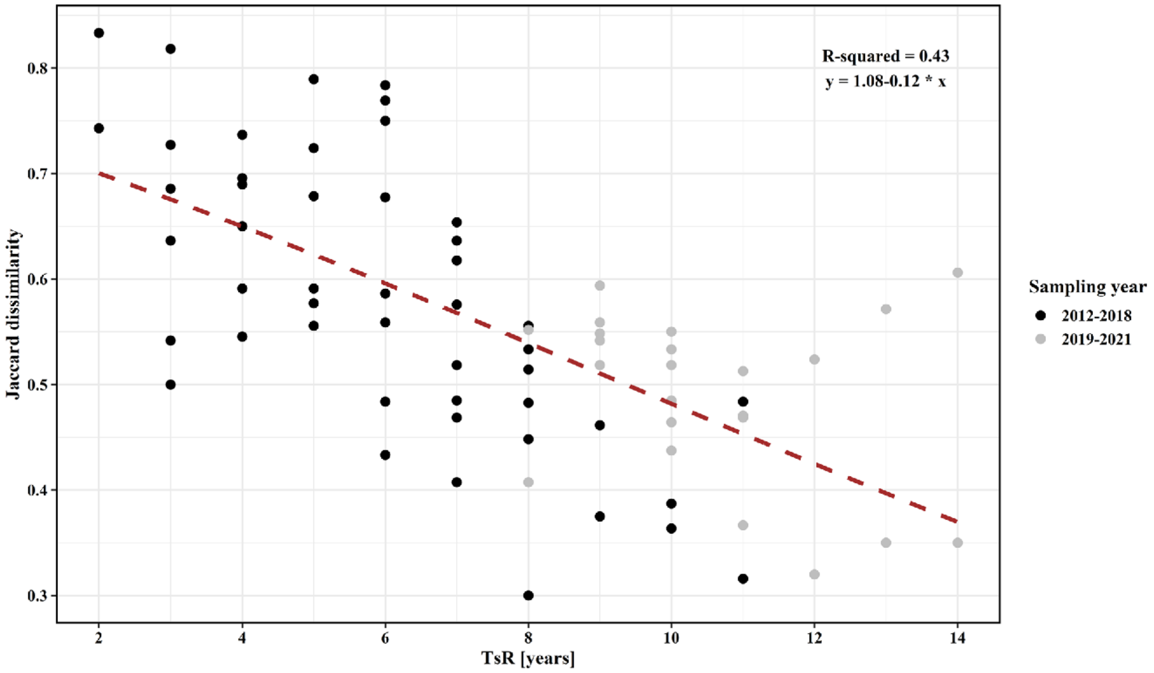

**Fig. 4** Generalised linear model of Jaccard dissimilarities between consecutive years per sampling site. Black dots = samples collected prior to the dry summer in 2018. Grey dots = samples collected following dry summer in 2018

*Glyphotaelius pellucidus* (glyppell) and Ephemeropterans, e.g. *Ephemera danica* (ephedani) and *Baetis rhodani* (baetrhod) belong to this second group.

The indicator species' frequency of occurrence across sampling sites mirrors their trends in abundance (Fig. 6b). The first species to disappear from all sites is *C. dipterum*, closely followed by the Coleopteran species, while *R. balthica* and *Asellus aquaticus* remain in the system during the complete sampling period but are found at less sites over time. On the other hand, *B. rhodani* and *E. danica* only enter the system five and six years after restoration, respectively. *Gammarus pulex* was present at one site starting the first year after restoration and at all sites from the seventh year onward.

Next to the indicator species, a set of species was identified, that was found every year at nearly all sampling sites without exhibiting a negative or positive trend over time. In total, six taxa occurred in at least 50% of all samples, however, five of these were only identified to higher taxonomic levels: Ceratopogoninae gen. sp., Chironomidae gen. sp., Chironomini gen. sp., Tanypodinae gen. sp., Limnephilini gen. sp., *Limnephilus lunatus*. Thus, the taxa with increasing or decreasing abundance trends are embedded into a matrix of constantly present taxa.

#### *H4: Impact of riparian vegetation*

The indicator species were put into context with the environmental variables via a multi-factorial analysis (MFA) (Fig. 7). The environmental variables that best explained their variation in abundance (limited to the indicator species) were identified using a second forward selection that excluded TsR as variable. The most important parameters influencing changes in indicator species abundance were identified to be shade ($p = 0.002$), conductivity ($p = 0.002$), the proportion of gravel/stones ($p = 0.002$), sand/sludge ($p = 0.002$), loam ($p = 0.002$) and pH ($p = 0.020$) (Table 3). Only these environmental variables were used in the MFA. Species abundances were displayed as gradient arrows since the direction of change in abundance was of major interest. The "increasing" species are clearly separated from the "decreasing" species, pointing to the left and the right side of the MFA, respectively. The majority of the "increasing" species is positively correlated with the gradient of shade level and, as a group, 40% of the variance is explained (Dim.1 = 0.40). On the other hand, the majority of the "decreasing" species is positively correlated with conductivity and 67% of the variance is explained (Dim.1 = 0.67). According to the correlation matrix (Additional file 5: Table S1), shade has the highest positive correlation with *P. olivacea* (prodoliv) ($r = 0.37$) and *G. pulex* (gammpule) ($r = 0.34$). *R. balthica*

**Fig. 5** RDA on Bray–Curtis dissimilarities of log(x + 1) transformed community data. The sampling sites are oriented along the environmental gradients, which mostly influence their community composition. Figures per sampling site are shown in Additional file 1: Figure S2

**Table 2** Results of the forward selection of the RDA including the complete dataset

| Variable | $R^2$ adj | Df | AIC | *F* | Pr (> *F*) |
|---|---|---|---|---|---|
| TsR | 0.113 | 1 | 347.83 | 11.02 | 0.002 |
| gravel/stones | 0.140 | 1 | 346.27 | 3.51 | 0.002 |
| shade | 0.162 | 1 | 345.16 | 3.01 | 0.002 |
| sand/sludge | 0.176 | 1 | 344.78 | 2.67 | 0.002 |
| POM | 0.185 | 1 | 344.79 | 1.87 | 0.008 |
| loam | 0.193 | 1 | 344.96 | 1.68 | 0.028 |

(radibalt) has a weak negative correlation with shade ($r = -0.27$). Conductivity is positively correlated with *C. dipterum* (cloedipt) ($r = 0.49$) and *Agabus didymus* ad. (agabdiad) ($r = 0.34$) and weakly negative with *G. pulex* (gammpule) ($r = -0.19$) and *Hemerodromia* sp. (hemesp) ($r = -0.16$). The highest positive correlation with gravel/stone was found for *H. angustipennis* (hydrangu) ($r = 0.48$) and *Agabus* sp. lv. (agabsp) ($r = 0.44$).

## Discussion

### H1: Community variability decreases with time since restoration

Our first hypothesis was confirmed. The results revealed a temporal gradient of community development. Species numbers increase mostly within the first five years after restoration. As time progresses, the distance between communities, thus the variation in species assemblages decreases. The initial distance between communities is likely the result of the sites being recolonised from different population sources and at different speeds. As the sampling sites mature, species can establish more populations and disperse across all tributaries of the Boye. Previous studies addressing successional processes in ponds, temporary wetlands and lakes [7, 26, 52] observed similar patterns and described initial colonisation after restoration to be fast, while the habitat specific assemblages and higher taxa diversity developed later.

Over time, dissimilarities between sampling years decrease, with the largest decrease between years one and eight after restoration. Thereafter, community

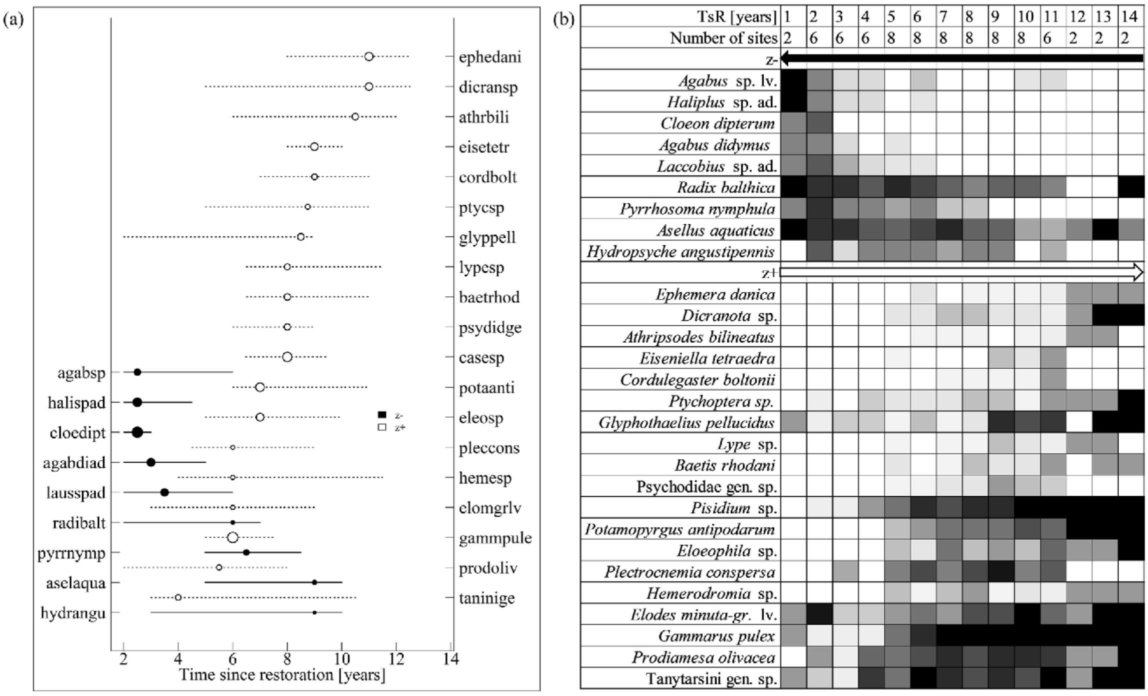

**Fig. 6** **a** TITAN Analysis of community data with time since restoration (TsR) as gradient with a reliability and purity cut-off of 0.9 (bootstraps = 1000). On the left-hand side, taxa with a decreasing trend in abundance are given (black dots, continuous line, z− ). On the right-hand side, taxa with an increasing trend in abundance are shown (white dots, dashed line, z+). The size of the dots shows the z scores. Higher z scores result in larger dots and demonstrate a larger indicator potential. **b** Heat map of frequency of occurrence across sampling sites per year since restoration. Black boxes = 100%, white boxes = 0%. For explanations of the species abbreviations see Additional file 4: Table S1

variability remains at a lower degree. Two major outliers of high variability more than 10 years after restoration are striking: dissimilarity of communities sampled in year 12/13, and 13/14 was high at sites along the Kirchschemmsbach. Increased community dissimilarity in the sampling period past 2018 was also observed for other sites, albeit to a lower degree. These observations are related to the very warm and dry summer 2018, the hottest summer in Germany since 2003, with 75 summer days above 25 °C [11]. As a result, many streams fell (partly) dry, which caused especially hololimnic species to vanish. They spend their complete life cycle in the water column and therefore rely on a constant flow of water. The conditions for the subsequent recolonisation, however, have greatly improved compared to the time 15 years ago, as benthic invertebrate populations have meanwhile colonised most of the Boye catchment.

In contrast to communities of temporary streams, which are adapted to unstable conditions, seasonal streambed drying can have detrimental effects on the community of usually permanent streams. One of the known consequences is the reduction of aquatic diversity, due to the loss of ill-adapted taxa to drying [56]. For example, Iversen et al. [21] found *G. pulex* and many Trichoptera species to disappear from stream sections that dried out for several months. Species abundance and richness were found to decline in restored and near-natural low mountain range streams of North Rhine-Westphalia following streambed drying but also extreme floods [30]. With climate change and anthropogenic water abstraction, the number of streams undergoing drying events and the duration of such events are expected to increase in the future [16]. These changes will undoubtedly affect biological communities that lack adaptations to such conditions. We conclude that while communities establish a certain degree of stability eight years after restoration, they remain subject to natural variation, which can be greatly increased by extreme heat and streambed drying [1, 30]. Previous research predicted restoration impacts on the invertebrate community about five years following restoration [38, 72]. While the timeframe for community recovery is dependent on various factors, the results highlight the need for continuous data to distinguish restoration effects on macroinvertebrate communities from natural variation unrelated to restoration [30, 34, 40].

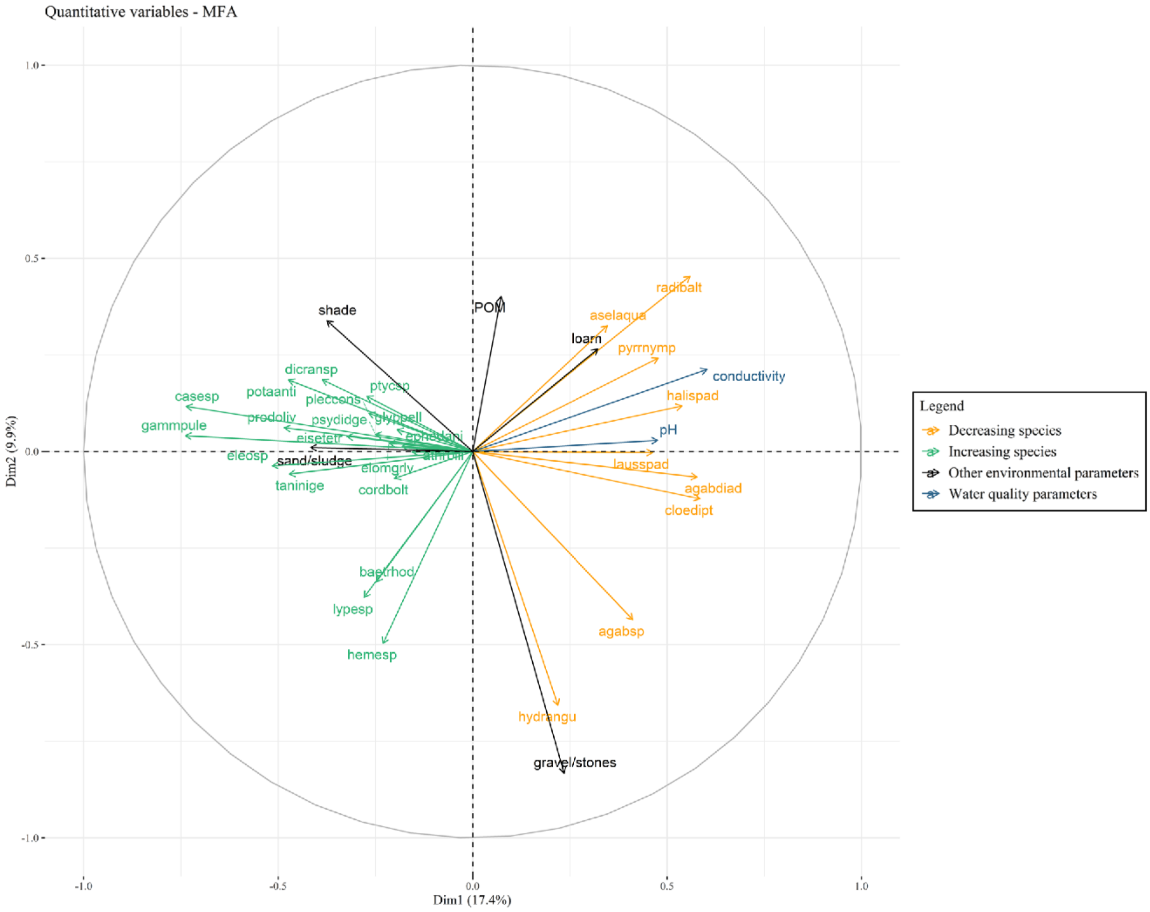

**Fig. 7** Multi-factorial analysis (MFA) of the most important explanatory variables influencing abundances of indicator species either showing an increasing or a decreasing trend with time since restoration

### *H2: Habitat development after restoration and impact on community succession*

Our second hypothesis that hydromorphological restoration initiates the development of substrate diversity, was confirmed as well. Once the streams were not transporting wastewater anymore, the removal of bank reinforcements was a major restoration measure conducted at all Boye tributaries. Furthermore, the stream channels were changed from straightened to sinuate or semi-meandering. Consequently, flow velocities were reduced. This causes a change in substrate proportions as the stream matures, with an increase in the proportion of sand, which characterizes lowland streams in the area [49]. Indeed, our results demonstrate that the proportion of sand/sludge increases with time since restoration. The proportion of stones is negatively correlated with the proportion of sand, which suggests that sand aggregated on top of the stones that were used as a replacement of the former concrete bed. Accordingly, the community composition changed from stone-preferring to sand-preferring species, e.g. *Ephemera danica*.

**Table 3** Results of the RDA forward selection of variables used in MFA for the indicator species

| Variable | $R^2$ adj | Df | AIC | *F* | Pr (> *F*) |
|---|---|---|---|---|---|
| conductivity | 0.050 | 1 | 299.94 | 5.11 | 0.002 |
| shade | 0.098 | 1 | 296.72 | 5.19 | 0.002 |
| gravel/stones | 0.138 | 1 | 294.02 | 4.60 | 0.002 |
| sand/sludge | 0.167 | 1 | 292.23 | 3.63 | 0.002 |
| loam | 0.191 | 1 | 290.79 | 3.25 | 0.002 |
| pH | 0.205 | 1 | 290.36 | 2.26 | 0.020 |

Verdonschot et al. [64] found that in lowland streams an increase in sand cover has a positive effect on the diversity of Ephemeroptera, Plecoptera and Trichoptera (EPT). Though sand supports low species richness and abundance, it still maintains a unique macroinvertebrate species assembly [74]. In general, the species assemblage is closely related to the available substrates. This is due to the number of niches available and the amount of ecosystem functions that need to be filled by various species. Thus, several studies have shown that species diversity increases with habitat and food source heterogeneity [17, 25, 46, 64].

The level of conductivity was a major driver for the species abundances. Conductivity decreases at least at some sites over time. High conductivity is an analogue for high salinity and is commonly found in urban streams, due to their high nutrient input [9]. Salts that settled in the stream's sediment, while wastewater was still transported within the stream, causing the high conductivity in the beginning of our study. Few species can cope with such conditions and others will only settle once conductivity is reduced [8]. In addition, during restoration, extra amounts of salts may have entered the streams due to the construction works. Once succession starts, the salts are constantly washed out from the watercourse and the sediment, causing conductivity to decrease over time.

#### *H3: Early colonising species vanish with habitat succession*

The third hypothesis was confirmed. We identified 28 indicator species as either increasing or decreasing with time since restoration. Only 9 species decrease, compared to 19 species that increase. This additionally demonstrates the general increase of diversity and taxa richness, as several species successfully establish populations. Less species are lost over time as stable populations develop. The decreasing species include *C. dipterum* (Ephemeroptera), several Coleoptera species and the Odonata *Pyrrhosoma nymphula*. All these species are active fliers with a good dispersal ability in their adult stage and thus colonised the newly created habitats quickly. In addition, the open habitat conditions of freshly restored streams are well suited for these species. The lack of riparian vegetation causes macrophytes to grow and water temperatures to increase, depicting a suitable habitat for *C. dipterum*, which prefers warm water and feeds on periphyton [54]. The Coleoptera species and *P. nymphula* also favour open landscapes and are predominantly predators. They benefit from quickly colonising r-strategists adapted to unstable conditions, e.g. Chironomidae. Westveer et al. [69] showed that r-strategists are the first to colonise restored streams, while k-strategists arrive later. Hence, certain species are specialized on settling in freshly restored habitats and leave as habitats mature [72]. Some subfamilies of Chironomidae larvae were found in more than 50% of all samples, not exhibiting an either increasing or decreasing trend over time. They are generally high abundant in streams and many species are tolerant to varying water conditions [32]. Limnephilini gen. sp. and one species from this taxa group, *Limnephilus lunatus*, were also abundant across most of the samples. This underlines the good dispersability of the species and hints on its generalist character; these factors potentially increase the chance on successful colonisation of new niches. The fact that only few taxa were found in more than half of the samples highlights the pronounced differences between stream communities.

The disappearance of some of the first colonising species in maturing streams is likely to be caused by two factors that add to each other. First, once riparian vegetation has established, streams are increasingly shaded, water temperatures decrease and input of particulate organic material (POM) into the stream increases. Consequently, the habitat becomes unsuitable for many of the first colonisers, e.g. grazing species because higher shading reduces biofilms growth. Instead, new niches become available, which can be occupied by a larger number of other species and many of the late colonisers are accordingly associated to shaded sites (Fig. 7). In addition, late colonisers may compete for space and food with the pioneer species. For example, *A. aquaticus* may have survived under the harsh conditions prevailing in polluted water, as it was present in the streams directly after restoration [20, 21], while other shredders like *G. pulex* had to immigrate afterwards. As they colonise similar substrates and share the same food source, they are likely to compete for space and food. This could explain the decrease of *A. aquaticus* and the increase of *G. pulex*.

Another tolerant species that is present from the first year after restoration onward is *R. balthica* (Gastropoda). Due to its low dispersal capabilities, the species may have survived the harsh conditions within the stream and was present prior to restoration. Another theory for its early occurrence is that the eggs were carried to the restored sites via other vectors, e.g. waterfowl [7, 61]. Over time, the abundance of *R. balthica* decreases, which demonstrates that the habitats become increasingly unsuitable for grazing species.

Many of the increasing species belong to the orders Diptera, Ephemeroptera and Trichoptera, which depend on the presence of suitable habitats. As the proportion of shade and sand increases, the abundance of sand-burrowing, active filter feeding species, e.g. *E. danica* increases as well. The growing riparian vegetation provides additional food sources, adding coarse particulate organic matter, e.g. leaves, to the stream, favouring for example *G. pellucidus*. The species has spread to most of the sampling sites in the ninth year following restoration, likely due to the increase in available food sources and riparian vegetation that is needed for egg laying.

The strong overall increase in species richness and the change of indicator species over time reflects the current maturation state of the restored streams, from which water managers could judge the progress towards good ecological status.

Urban streams pose particular challenges to restoration, ranging from continuous pollution to the absence of recolonisation sources. Consequently, and in contrast to our findings, Stranko et al. [58] observed the number of mayflies and other intolerant macroinvertebrate species to decline in urban restored sites within 10 years of monitoring and eventually no effect of restoration actions on community composition. However, our findings show that if dispersal capacities and the creation of suitable habitats are permitted to guide local development, biodiversity can be improved and restored, albeit slowly, in urban streams.

#### *H4: Impact of riparian vegetation*

In line with our fourth hypothesis, the percentage of shade increases with time since restoration, which shows the succession of riparian forest. Trees stabilize the riverbanks and provide a source for coarse organic material and deadwood [50, 62]. The presence of deadwood increases habitat heterogeneity and thereby supports a higher species diversity [23], while shading decreases water temperatures [10, 24]. This allows especially heat sensitive species to colonise respective sites and is generally important to protect the community from extreme heat. We identified the percentage shade to be an important driver for species abundance. In general, the presence of woody riparian cover has a strong effect on riverine macroinvertebrate communities [47]. Although the authors found effects of woody riparian cover to be greater in rural than in urban streams, 100% woody riparian cover still improved the ecological status of urban streams. Shredders benefit from the input of particulate organic matter, while primary production decreases, which reduces the abundance of grazers [39].

## Conclusion

We disentangled the recolonisation process of restored urban streams. It took almost a decade after wastewater was removed and hydromorphological restoration was completed to develop a stable macroinvertebrate community. While the communities underlie continuous shifts, the size of these variations peaks in the first eight years following restoration, when niches develop and are stepwise occupied by invading species. The time since restoration is central for the development of these niches. At restored sites, new instream habitats become available, largely triggered by the succession of the stream's surroundings, i.e. the growth of woody vegetation on the stream banks. Thus, habitat development as a result of maturation over time is a key driver for successful recolonisation of restored streams.

Our results underline the potential for the restoration of urban streams. Despite numerous challenges including strong pollution prior to restoration, limited space and restricted recolonisation sources, a distinct succession towards a community adapted to stable conditions was observed in all restored sites. Targets for urban stream restoration should therefore be ambitious and key factors for habitat development, in particular the development of riparian vegetation, should be enabled.

### Abbreviations

| | |
|---|---|
| CPOM | Coarse particulate organic matter |
| GLM | Generalised linear model |
| LPTP | Living parts of terrestrial plants |
| MFA | Multi-factorial analysis |
| NMDS | Non-metric multidimensional scaling |
| perMANOVA | Permutational multivariate analysis of variance |
| POM | Particulate organic matter |
| RDA | Redundancy analysis |
| TsR | Time since restoration |
| TsW | Time since wastewater was removed |

## Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s12302-023-00756-x.

**Additional file 1: Table S1.** Spearman's Rank coefficients of all environmental variables.

**Additional file 2: Figure S1.** NMDS of log-transformed community data per sampling site, sampling years connected. Time since restoration was added as an overlay (red arrow).

**Additional file 3: Table S1.** Records on streambed drying in the Boye catchment between 2018 and 2020. Information on the periods of streambed drying in the Boye were collected unstandardized from the local water board (Emschergenossenschaft) and colleagues from the University of Duisburg-Essen. All the information was recorded in either August or September of the respective years.

**Additional file 4: Table S1.** Explanation of species abbreviations (*ad* adult, *lv* larvae, *sp* species, *gen* genus).

**Additional file 5: Table S1.** Spearman's Rank coefficients of indicator species and major environmental variables (for explanations of the species abbreviations refer to Additional file 4: Table S1).

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### Author contributions

AL, SG and DH designed the study; AL organised and conducted sample collection and processing, with contributions by SG; AL collected the data; SG analysed the data and led the writing of the manuscript. All authors contributed to the drafts and approved the final version.

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### Availability of data and materials

The datasets used and analysed during this study are available from the corresponding author on reasonable request.

## Declarations

### Competing interests

The authors declare no competing interests.

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## Publisher's Note

# Supplementary Materials

## Appendix S1:

Table S1. Spearman's Rank coefficients of all environmental variables

| Variables | TsR | shade | pH | conductivity | oxygen | LPTP | gravel/stones | sand/sludge | macrophytes | POM | algae | loam |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **TsR** | 1.000 | 0.400 | -0.340 | -0.366 | 0.037 | -0.282 | -0.198 | 0.369 | 0.071 | -0.192 | -0.154 | -0.304 |
| **shade** | 0.400 | 1.000 | -0.059 | 0.006 | 0.098 | -0.437 | -0.221 | 0.268 | -0.023 | 0.051 | -0.055 | 0.013 |
| **pH** | -0.340 | -0.059 | 1.000 | 0.163 | 0.125 | -0.003 | 0.063 | -0.057 | -0.063 | 0.067 | 0.118 | -0.030 |
| **conductivity** | -0.366 | 0.006 | 0.163 | 1.000 | 0.030 | 0.155 | -0.002 | -0.054 | -0.075 | 0.086 | 0.070 | 0.220 |
| **oxygen** | 0.037 | 0.098 | 0.125 | 0.030 | 1.000 | -0.220 | 0.141 | -0.065 | 0.042 | -0.021 | -0.030 | -0.185 |
| **LPTP** | -0.282 | -0.437 | -0.003 | 0.155 | -0.220 | 1.000 | 0.288 | -0.149 | -0.250 | -0.105 | 0.363 | 0.229 |
| **gravel/stones** | -0.198 | -0.221 | 0.063 | -0.002 | 0.141 | 0.288 | 1.000 | -0.098 | -0.448 | -0.166 | 0.162 | 0.018 |
| **sand/sludge** | 0.369 | 0.268 | -0.057 | -0.054 | -0.065 | -0.149 | -0.098 | 1.000 | -0.506 | -0.129 | -0.237 | 0.008 |
| **macrophytes** | 0.071 | -0.023 | -0.063 | -0.075 | 0.042 | -0.250 | -0.448 | -0.506 | 1.000 | -0.434 | -0.193 | -0.222 |
| **POM** | -0.192 | 0.051 | 0.067 | 0.086 | -0.021 | -0.105 | -0.166 | -0.129 | -0.434 | 1.000 | -0.095 | -0.057 |
| **algae** | -0.154 | -0.055 | 0.118 | 0.070 | -0.030 | 0.363 | 0.162 | -0.237 | -0.193 | -0.095 | 1.000 | 0.580 |
| **loam** | -0.304 | 0.013 | -0.030 | 0.220 | -0.185 | 0.229 | 0.018 | 0.008 | -0.222 | -0.057 | 0.580 | 1.000 |

## Appendix S2:

Figure S1. NMDS of log-transformed community data per sampling site, sampling years connected. Time since restoration was added as an overlay (red arrow).

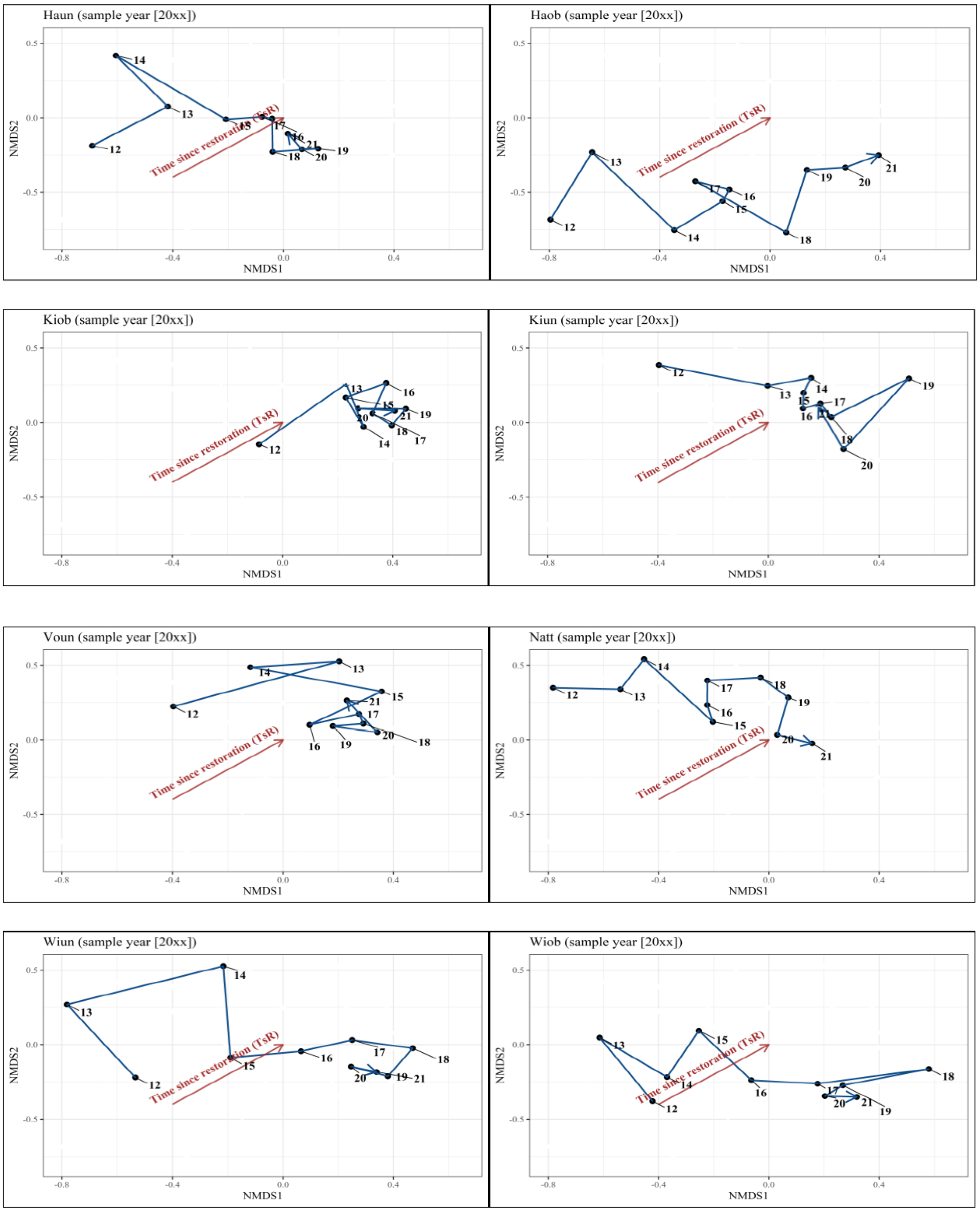
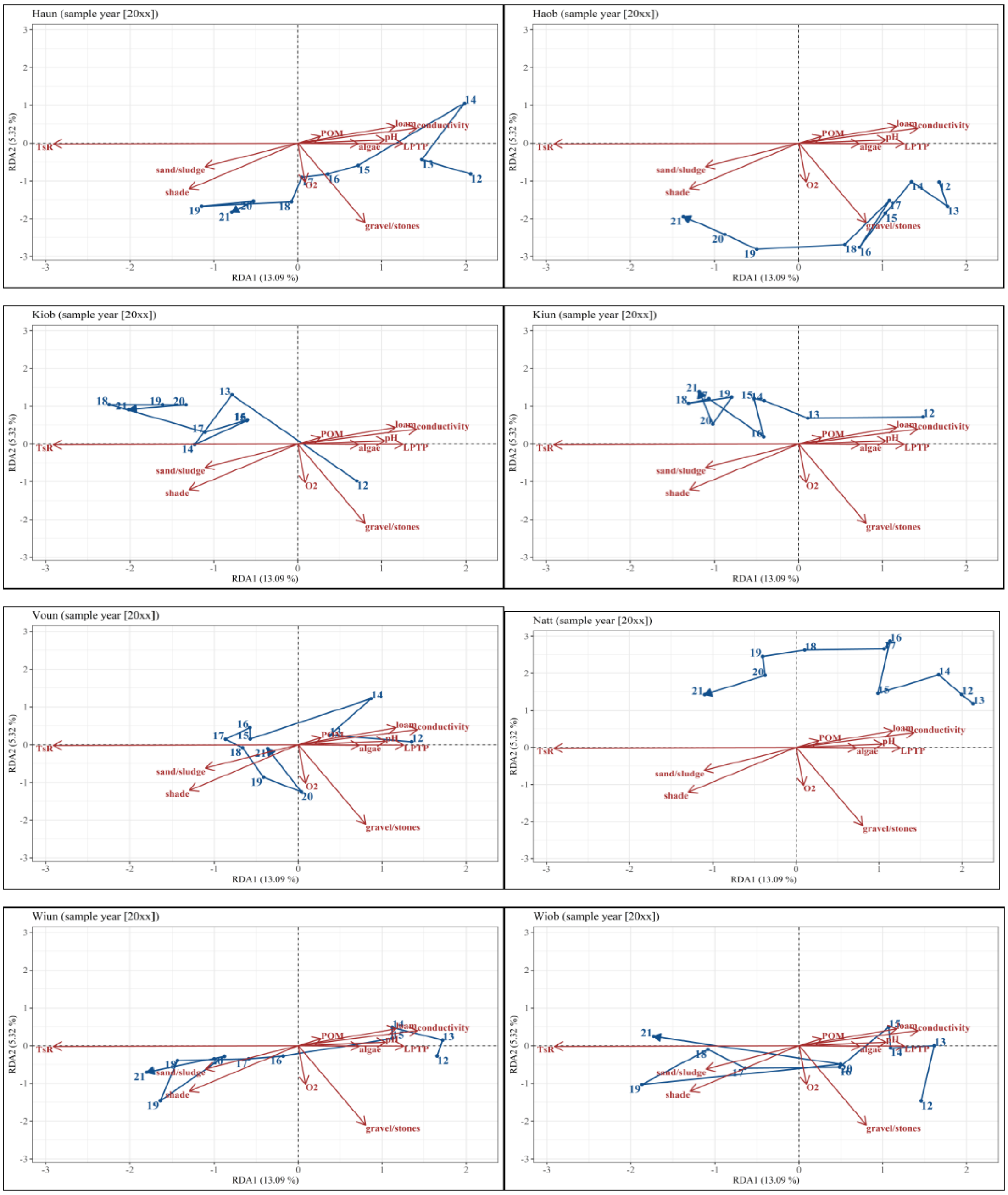


Figure S2. RDA of log-transformed community data per sampling site. Site Ids are shown above each graph. The numbers depict the sampling year, e.g. 12 = 2012.



Haun (sample year [20xx])

Haob (sample year [20xx])

Kiob (sample year [20xx])

Kiun (sample year [20xx])

Voun (sample year [20xx])

Natt (sample year [20xx])

Wiun (sample year [20xx])

Wiob (sample year [20xx])

**Appendix S3:**

Table S1. Records on streambed drying in the Boye catchment between 2018 and 2020. Information on the periods of streambed drying in the Boye were collected unstandardized from the local water board (Emschergenossenschaft) and colleagues from the University of Duisburg-Essen. All the information was recorded in either August or September of the respective years.

| Site | 2018 | 2019 | 2020 |
|---|---|---|---|
| Kiob | Continuous flow | Continuous flow | Continuous flow |
| Kiun | Continuous flow | Continuous flow | Continuous flow |
| Voun | No information available | Flow recorded upstream | Minimal flow |
| Haob | Continuous flow | Continuous flow | Continuous flow |
| Haun | Continuous flow | No information available; stagnant at mouth | Continuous flow |
| Nat | Dry (September) | Minimal flow/ dry | Continuous flow |
| Wiob | Minimal flow/ dry | Standing water in August | Continuous flow |
| Wiun | Minimal flow/ dry | Flow/ standing water | Dry |

**References:**

Emschergenossenschaft (EGLV):

- W. Sauer
- S. Podzielny
- M. Koudaimi
- T. Korte
- M. Semrau

University of Duisburg-Essen:

- J. Enß

**Appendix S4:**

Table S1. Explanation of species abbreviations (ad. = adult, lv. = larvae, sp. = species, gen. = genus)

| Short form | Species name |
|---|---|
| agabsp | *Agabus* sp. lv. |
| halispad | *Haliplus* sp. ad. |
| cloedipt | *Cloeon dipterum* |
| agabdiad | *Agabus didymus* ad. |
| lausspad | *Laccobius* sp. ad. |
| radibalt | *Radix balthica* |
| pyrrnymp | *Pyrrhosoma nymphula* |
| aselaqua | *Asellus aquaticus* |
| hydrangu | *Hydropsyche angustipennis angustipennis* |
| ephedani | *Ephemera danica* |
| dicransp | *Dicranota* sp. |
| athrbili | *Athripsodes bilineatus* |
| eisetetr | *Eiseniella tetraedra* |
| cordbolt | *Cordulegaster boltonii* |
| ptycsp | *Ptychoptera* sp. |
| glyppell | *Glyphotaelius pellucidus* |
| lypesp | *Lype* sp. |
| baetrhod | *Baetis rhodani* |
| psydidge | Psychodidae gen. sp. |
| casesp | *Pisidium* sp. |
| potaanti | *Potamopyrgus antipodarum* |
| eleosp | *Eloeophila* sp. |
| pleccons | *Plectrocnemia conspersa conspersa* |
| hemesp | *Hemerodromia* sp. |
| elomgrlv | *Elodes minuta-gr.* lv. |
| gammpule | *Gammarus pulex* |
| prodoliv | *Prodiamesa olivacea* |
| taninige | Tanytarsini gen. sp. |

## Appendix S5:

Table S1. Spearman's Rank coefficients of indicator species and major environmental variables (for explanations of the species abbreviations refer to Appendix S4: Table S1)

| **Species** | **agabsp** | **cloedipt** | **agabdiad** | **halispad** | **lausspad** | **pyrrnymp** | **aselaqua** | **radibalt** | **hydrangu** | **ephedani** | **athrbili** | **dicransp** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **agabsp** | 1.000 | 0.500 | 0.406 | 0.040 | 0.087 | -0.007 | -0.076 | -0.003 | 0.208 | -0.058 | -0.046 | -0.088 |
| **cloedipt** | 0.500 | 1.000 | 0.496 | 0.070 | 0.206 | 0.019 | -0.039 | 0.138 | 0.074 | -0.057 | -0.045 | -0.087 |
| **agabdiad** | 0.406 | 0.496 | 1.000 | 0.410 | 0.166 | 0.180 | 0.043 | 0.007 | 0.068 | -0.067 | -0.053 | -0.101 |
| **halispad** | 0.040 | 0.070 | 0.410 | 1.000 | 0.174 | 0.124 | 0.185 | 0.202 | -0.031 | -0.063 | -0.050 | -0.095 |
| **lausspad** | 0.087 | 0.206 | 0.166 | 0.174 | 1.000 | 0.050 | -0.077 | -0.006 | 0.073 | -0.077 | -0.061 | -0.116 |
| **pyrrnymp** | -0.007 | 0.019 | 0.180 | 0.124 | 0.050 | 1.000 | 0.095 | 0.111 | 0.096 | -0.075 | -0.015 | -0.131 |
| **aselaqua** | -0.076 | -0.039 | 0.043 | 0.185 | -0.077 | 0.095 | 1.000 | 0.185 | -0.057 | -0.123 | -0.095 | -0.053 |
| **radibalt** | -0.003 | 0.138 | 0.007 | 0.202 | -0.006 | 0.111 | 0.185 | 1.000 | -0.071 | -0.062 | -0.047 | -0.086 |
| **hydrangu** | 0.208 | 0.074 | 0.068 | -0.031 | 0.073 | 0.096 | -0.057 | -0.071 | 1.000 | -0.079 | -0.014 | -0.109 |
| **ephedani** | -0.058 | -0.057 | -0.067 | -0.063 | -0.077 | -0.075 | -0.123 | -0.062 | -0.079 | 1.000 | 0.679 | -0.009 |
| **athrbili** | -0.046 | -0.045 | -0.053 | -0.050 | -0.061 | -0.015 | -0.095 | -0.047 | -0.014 | 0.679 | 1.000 | 0.023 |
| **dicransp** | -0.088 | -0.087 | -0.101 | -0.095 | -0.116 | -0.131 | -0.053 | -0.086 | -0.109 | -0.009 | 0.023 | 1.000 |
| **pleccons** | -0.057 | -0.080 | -0.093 | -0.088 | -0.056 | -0.111 | -0.082 | -0.060 | -0.032 | -0.094 | -0.074 | -0.092 |
| **cisetetr** | -0.039 | -0.059 | -0.068 | -0.064 | -0.079 | -0.091 | -0.151 | -0.055 | -0.065 | -0.068 | -0.054 | -0.096 |
| **glyppell** | -0.041 | -0.079 | 0.107 | 0.460 | 0.055 | -0.108 | 0.141 | 0.125 | -0.074 | -0.064 | -0.023 | -0.067 |
| **cordbolt** | -0.033 | -0.046 | -0.053 | -0.050 | -0.061 | -0.071 | -0.102 | -0.045 | -0.006 | -0.053 | -0.042 | -0.081 |
| **bactrhod** | -0.050 | -0.066 | -0.071 | -0.072 | -0.088 | -0.097 | -0.155 | -0.071 | 0.000 | 0.160 | 0.092 | -0.089 |
| **lypesp** | -0.078 | -0.078 | -0.090 | -0.085 | -0.104 | -0.120 | -0.174 | -0.085 | 0.030 | 0.015 | 0.128 | -0.069 |
| **ptycsp** | -0.044 | -0.053 | -0.061 | -0.057 | -0.068 | -0.080 | -0.104 | -0.054 | -0.044 | -0.053 | -0.039 | -0.077 |
| **psydidge** | -0.037 | -0.081 | -0.094 | -0.089 | -0.108 | -0.093 | -0.070 | -0.080 | -0.054 | -0.094 | -0.068 | -0.095 |
| **potaanti** | -0.080 | -0.079 | -0.092 | -0.086 | -0.103 | -0.104 | -0.140 | -0.074 | -0.083 | 0.040 | -0.018 | 0.433 |
| **casesp** | -0.053 | -0.096 | -0.111 | -0.104 | -0.127 | -0.134 | -0.157 | -0.094 | -0.124 | -0.056 | -0.060 | 0.334 |
| **elomgrlv** | -0.063 | -0.086 | -0.086 | -0.061 | 0.064 | -0.082 | 0.113 | -0.054 | -0.089 | -0.067 | -0.042 | -0.027 |
| **eleosp** | -0.089 | -0.094 | -0.109 | -0.102 | -0.121 | -0.145 | -0.180 | -0.100 | -0.110 | 0.025 | 0.027 | 0.137 |
| **hemesp** | 0.013 | -0.066 | -0.076 | -0.072 | -0.088 | -0.088 | -0.131 | -0.074 | 0.185 | -0.027 | 0.015 | -0.068 |
| **gammpule** | -0.100 | -0.128 | -0.142 | -0.125 | -0.167 | -0.155 | -0.051 | -0.122 | -0.100 | -0.008 | 0.011 | 0.068 |
| **taninige** | -0.060 | -0.106 | -0.157 | -0.135 | -0.168 | 0.293 | -0.116 | 0.030 | 0.026 | 0.020 | 0.041 | 0.428 |
| **prodoliv** | -0.090 | -0.134 | 0.043 | -0.066 | -0.135 | -0.071 | -0.032 | -0.145 | -0.092 | -0.128 | -0.103 | 0.173 |
| **conductivity** | 0.250 | 0.489 | 0.340 | 0.121 | 0.143 | 0.064 | 0.133 | 0.141 | 0.010 | -0.111 | -0.085 | -0.126 |
| **pH** | 0.059 | 0.311 | 0.261 | 0.165 | 0.082 | 0.138 | -0.121 | 0.210 | 0.097 | 0.108 | 0.096 | -0.087 |
| **loam** | -0.023 | -0.037 | -0.037 | 0.333 | 0.128 | 0.050 | 0.112 | 0.295 | -0.113 | -0.097 | -0.077 | -0.055 |
| **POM** | -0.105 | 0.064 | 0.067 | 0.075 | -0.012 | -0.050 | 0.065 | 0.004 | -0.159 | -0.152 | -0.160 | 0.039 |
| **sand/sludge** | -0.159 | -0.071 | -0.121 | -0.131 | -0.117 | -0.024 | -0.301 | -0.146 | -0.044 | 0.031 | 0.006 | 0.267 |
| **gravel/stones** | 0.439 | 0.139 | 0.179 | 0.112 | -0.014 | -0.083 | -0.071 | 0.026 | 0.482 | -0.166 | -0.127 | -0.205 |
| **shade** | -0.193 | -0.080 | -0.065 | -0.006 | -0.156 | 0.189 | -0.181 | -0.268 | -0.200 | -0.030 | 0.035 | 0.067 |

Table S1. Spearman's Rank coefficients of indicator species and major environmental variables (for explanations of the species abbreviations refer to Appendix S4: Table S1) (continued)

| Species | pleccons | eisetetr | glyppell | cordbolt | baetrhod | lypesp | ptycsp | psydidge | potaanti | casesp | elomgrlv | eleosp |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| agabsp | -0.057 | -0.039 | -0.041 | -0.033 | -0.050 | -0.078 | -0.044 | -0.037 | -0.080 | -0.053 | -0.063 | -0.089 |
| cloedipt | -0.080 | -0.059 | -0.079 | -0.046 | -0.066 | -0.078 | -0.053 | -0.081 | -0.079 | -0.096 | -0.086 | -0.094 |
| agabdiad | -0.093 | -0.068 | 0.107 | -0.053 | -0.071 | -0.090 | -0.061 | -0.094 | -0.092 | -0.111 | -0.086 | -0.109 |
| halispad | -0.088 | -0.064 | 0.460 | -0.050 | -0.072 | -0.085 | -0.057 | -0.089 | -0.086 | -0.104 | -0.061 | -0.102 |
| lausspad | -0.056 | -0.079 | 0.055 | -0.061 | -0.088 | -0.104 | -0.068 | -0.108 | -0.103 | -0.127 | 0.064 | -0.121 |
| pyrrnymp | -0.111 | -0.091 | -0.108 | -0.071 | -0.097 | -0.120 | -0.080 | -0.093 | -0.104 | -0.134 | -0.082 | -0.145 |
| aselaqua | -0.082 | -0.151 | 0.141 | -0.102 | -0.155 | -0.174 | -0.104 | -0.070 | -0.140 | -0.157 | 0.113 | -0.180 |
| radibalt | -0.060 | -0.055 | 0.125 | -0.045 | -0.071 | -0.085 | -0.054 | -0.080 | -0.074 | -0.094 | -0.054 | -0.100 |
| hydrangu | -0.032 | -0.065 | -0.074 | -0.006 | 0.000 | 0.030 | -0.044 | -0.054 | -0.083 | -0.124 | -0.089 | -0.110 |
| ephedani | -0.094 | -0.068 | -0.064 | -0.053 | 0.160 | 0.015 | -0.053 | -0.094 | 0.040 | -0.056 | -0.067 | 0.025 |
| athrbili | -0.074 | -0.054 | -0.023 | -0.042 | 0.092 | 0.128 | -0.039 | -0.068 | -0.018 | -0.060 | -0.042 | 0.027 |
| dicransp | -0.092 | -0.096 | -0.067 | -0.081 | -0.089 | -0.069 | -0.077 | -0.095 | 0.433 | 0.334 | -0.027 | 0.137 |
| pleccons | 1.000 | 0.473 | 0.217 | 0.644 | -0.080 | 0.096 | 0.533 | 0.200 | 0.229 | 0.022 | 0.133 | 0.240 |
| eisetetr | 0.473 | 1.000 | 0.187 | 0.285 | -0.071 | -0.023 | 0.130 | 0.395 | 0.081 | 0.236 | -0.031 | 0.473 |
| glyppell | 0.217 | 0.187 | 1.000 | 0.103 | -0.052 | 0.041 | -0.002 | 0.164 | 0.010 | 0.010 | 0.129 | 0.224 |
| cordbolt | 0.644 | 0.285 | 0.103 | 1.000 | -0.053 | 0.128 | 0.573 | 0.452 | 0.504 | 0.072 | 0.082 | -0.058 |
| baetrhod | -0.080 | -0.071 | -0.052 | -0.053 | 1.000 | 0.633 | -0.002 | -0.038 | -0.052 | 0.024 | -0.089 | 0.217 |
| lypesp | 0.096 | -0.023 | 0.041 | 0.128 | 0.633 | 1.000 | -0.015 | -0.020 | 0.004 | 0.134 | 0.056 | 0.086 |
| ptycsp | 0.533 | 0.130 | -0.002 | 0.573 | -0.002 | -0.015 | 1.000 | 0.316 | 0.280 | 0.010 | 0.320 | -0.029 |
| psydidge | 0.200 | 0.395 | 0.164 | 0.452 | -0.038 | -0.020 | 0.316 | 1.000 | 0.195 | 0.089 | 0.236 | 0.089 |
| potaanti | 0.229 | 0.081 | 0.010 | 0.504 | -0.052 | 0.004 | 0.280 | 0.195 | 1.000 | 0.480 | 0.159 | -0.025 |
| casesp | 0.022 | 0.236 | 0.010 | 0.072 | 0.024 | 0.134 | 0.010 | 0.089 | 0.480 | 1.000 | -0.052 | 0.157 |
| elomgrlv | 0.133 | -0.031 | 0.129 | 0.082 | -0.089 | 0.056 | 0.320 | 0.236 | 0.159 | -0.052 | 1.000 | -0.101 |
| eleosp | 0.240 | 0.473 | 0.224 | -0.058 | 0.217 | 0.086 | -0.029 | 0.089 | -0.025 | 0.157 | -0.101 | 1.000 |
| hemesp | -0.080 | -0.040 | -0.044 | -0.022 | 0.232 | 0.477 | -0.051 | -0.057 | -0.091 | 0.278 | -0.086 | 0.036 |
| gammpule | 0.313 | 0.427 | 0.026 | -0.025 | 0.042 | 0.091 | 0.056 | -0.080 | -0.014 | 0.262 | 0.080 | 0.118 |
| taninige | 0.134 | 0.098 | 0.057 | 0.050 | -0.091 | 0.050 | -0.020 | -0.027 | 0.332 | 0.252 | -0.001 | 0.219 |
| prodoliv | -0.017 | 0.124 | -0.009 | -0.028 | 0.250 | 0.206 | -0.093 | 0.098 | 0.047 | 0.280 | -0.174 | 0.161 |
| conductivity | -0.053 | -0.067 | -0.072 | -0.014 | -0.164 | -0.161 | -0.011 | -0.009 | -0.019 | -0.154 | 0.091 | -0.152 |
| pH | -0.169 | -0.156 | 0.037 | -0.042 | 0.054 | -0.105 | 0.110 | -0.088 | 0.035 | -0.044 | 0.016 | -0.263 |
| loam | -0.118 | -0.100 | -0.067 | -0.078 | 0.072 | -0.131 | -0.088 | -0.045 | -0.133 | -0.110 | -0.139 | 0.117 |
| POM | 0.260 | 0.058 | 0.167 | 0.170 | -0.195 | -0.059 | 0.160 | -0.010 | -0.045 | -0.121 | -0.049 | 0.103 |
| sand/sludge | -0.131 | 0.068 | -0.111 | -0.096 | 0.121 | 0.100 | -0.024 | 0.146 | 0.123 | 0.383 | -0.171 | 0.190 |
| gravel/stones | 0.089 | -0.072 | 0.184 | 0.098 | 0.286 | 0.275 | -0.012 | -0.047 | -0.143 | -0.075 | -0.155 | -0.054 |
| shade | 0.191 | 0.235 | 0.011 | 0.036 | 0.194 | 0.041 | 0.092 | 0.160 | 0.039 | 0.234 | -0.065 | 0.169 |

Table S1. Spearman's Rank coefficients of indicator species and major environmental variables (for explanations of the species abbreviations refer to Appendix S4: Table S1) (continued)

| **Species** | **hemesp** | **gammpule** | **taninige** | **prodoliv** | **conductivity** | **pH** | **loam** | **POM** | **sand/sludge** | **gravel/stones** | **shade** |
|---:|---|---|---|---|---|---|---|---|---|---|---|
| **agabsp** | 0.013 | -0.100 | -0.060 | -0.090 | 0.250 | 0.059 | -0.023 | -0.105 | -0.159 | 0.439 | -0.193 |
| **cloedipt** | -0.066 | -0.128 | -0.106 | -0.134 | 0.489 | 0.311 | -0.037 | 0.064 | -0.071 | 0.139 | -0.080 |
| **agabdiad** | -0.076 | -0.142 | -0.157 | 0.043 | 0.340 | 0.261 | -0.037 | 0.067 | -0.121 | 0.179 | -0.065 |
| **halispad** | -0.072 | -0.125 | -0.135 | -0.066 | 0.121 | 0.165 | 0.333 | 0.075 | -0.131 | 0.112 | -0.006 |
| **lausspad** | -0.088 | -0.167 | -0.168 | -0.135 | 0.143 | 0.082 | 0.128 | -0.012 | -0.117 | -0.014 | -0.156 |
| **pyrrnymp** | -0.088 | -0.155 | 0.293 | -0.071 | 0.064 | 0.138 | 0.050 | -0.050 | -0.024 | -0.083 | 0.189 |
| **aselaqua** | -0.131 | -0.051 | -0.116 | -0.032 | 0.133 | -0.121 | 0.112 | 0.065 | -0.301 | -0.071 | -0.181 |
| **radibalt** | -0.074 | -0.122 | 0.030 | -0.145 | 0.141 | 0.210 | 0.295 | 0.004 | -0.146 | 0.026 | -0.268 |
| **hydrangu** | 0.185 | -0.100 | 0.026 | -0.092 | 0.010 | 0.097 | -0.113 | -0.159 | -0.044 | 0.482 | -0.200 |
| **ephedani** | -0.027 | -0.008 | 0.020 | -0.128 | -0.111 | 0.108 | -0.097 | -0.152 | 0.031 | -0.166 | -0.030 |
| **athrbili** | 0.015 | 0.011 | 0.041 | -0.103 | -0.085 | 0.096 | -0.077 | -0.160 | 0.006 | -0.127 | 0.035 |
| **dicransp** | -0.068 | 0.068 | 0.428 | 0.173 | -0.126 | -0.087 | -0.055 | 0.039 | 0.267 | -0.205 | 0.067 |
| **pleccons** | -0.080 | 0.313 | 0.134 | -0.017 | -0.053 | -0.169 | -0.118 | 0.260 | -0.131 | 0.089 | 0.191 |
| **cisetetr** | -0.040 | 0.427 | 0.098 | 0.124 | -0.067 | -0.156 | -0.100 | 0.058 | 0.068 | -0.072 | 0.235 |
| **glyppell** | -0.044 | 0.026 | 0.057 | -0.009 | -0.072 | 0.037 | -0.067 | 0.167 | -0.111 | 0.184 | 0.011 |
| **cordbolt** | -0.022 | -0.025 | 0.050 | -0.028 | -0.014 | -0.042 | -0.078 | 0.170 | -0.096 | 0.098 | 0.036 |
| **baetrhod** | 0.232 | 0.042 | -0.091 | 0.250 | -0.164 | 0.054 | 0.072 | -0.195 | 0.121 | 0.286 | 0.194 |
| **lypesp** | 0.477 | 0.091 | 0.050 | 0.206 | -0.161 | -0.105 | -0.131 | -0.059 | 0.100 | 0.275 | 0.041 |
| **ptycsp** | -0.051 | 0.056 | -0.020 | -0.093 | -0.011 | 0.110 | -0.088 | 0.160 | -0.024 | -0.012 | 0.092 |
| **psydidge** | -0.057 | -0.080 | -0.027 | 0.098 | -0.009 | -0.088 | -0.045 | -0.010 | 0.146 | -0.047 | 0.160 |
| **potaanti** | -0.091 | -0.014 | 0.332 | 0.047 | -0.019 | 0.035 | -0.133 | -0.045 | 0.123 | -0.143 | 0.039 |
| **casesp** | 0.278 | 0.262 | 0.252 | 0.280 | -0.154 | -0.044 | -0.110 | -0.121 | 0.383 | -0.075 | 0.234 |
| **elomgrlv** | -0.086 | 0.080 | -0.001 | -0.174 | 0.091 | 0.016 | -0.139 | -0.049 | -0.171 | -0.155 | -0.065 |
| **eleosp** | 0.036 | 0.118 | 0.219 | 0.161 | -0.152 | -0.263 | 0.117 | 0.103 | 0.190 | -0.054 | 0.169 |
| **hemesp** | 1.000 | 0.043 | 0.014 | 0.035 | -0.157 | 0.002 | -0.101 | -0.150 | 0.132 | 0.361 | 0.043 |
| **gammpule** | 0.043 | 1.000 | 0.027 | 0.025 | -0.190 | -0.168 | -0.156 | -0.090 | 0.059 | -0.103 | 0.341 |
| **taninige** | 0.014 | 0.027 | 1.000 | 0.141 | -0.046 | -0.097 | -0.154 | 0.059 | 0.175 | -0.014 | 0.123 |
| **prodoliv** | 0.035 | 0.025 | 0.141 | 1.000 | 0.223 | -0.098 | 0.016 | 0.009 | 0.407 | -0.084 | 0.368 |
| **conductivity** | -0.157 | -0.190 | -0.046 | 0.223 | 1.000 | 0.163 | 0.220 | 0.086 | -0.054 | -0.002 | 0.006 |
| **pH** | 0.002 | -0.168 | -0.097 | -0.098 | 0.163 | 1.000 | -0.030 | 0.067 | -0.057 | 0.063 | -0.059 |
| **loam** | -0.101 | -0.156 | -0.154 | 0.016 | 0.220 | -0.030 | 1.000 | -0.057 | 0.008 | 0.018 | 0.013 |
| **POM** | -0.150 | -0.090 | 0.059 | 0.009 | 0.086 | 0.067 | -0.057 | 1.000 | -0.129 | -0.166 | 0.051 |
| **sand/sludge** | 0.132 | 0.059 | 0.175 | 0.407 | -0.054 | -0.057 | 0.008 | -0.129 | 1.000 | -0.098 | 0.268 |
| **gravel/stones** | 0.361 | -0.103 | -0.014 | -0.084 | -0.002 | 0.063 | 0.018 | -0.166 | -0.098 | 1.000 | -0.221 |
| **shade** | 0.043 | 0.341 | 0.123 | 0.368 | 0.006 | -0.059 | 0.013 | 0.051 | 0.268 | -0.221 | 1.000 |

## Extent of Contribution

Cumulative thesis of Svenja M. Gillmann

### Author contributions

Title: *Habitat development and species arrival drive succession of the benthic invertebrate community in restored urban streams*

Authors: Gillmann, S.M., Hering, D., Lorenz, A.W.

Contributions:

- Conception - 70%
- Conduction of experimental work - 20%: field sampling in two years
- Data analysis -80 %
- Species identification - 30%
- Statistical analysis - 100%
- Writing the manuscript - 80%
- Revision of the manuscript - 90%

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# Chapter 2

## How tolerances, competition and dispersal shape benthic invertebrate colonisation in restored urban streams

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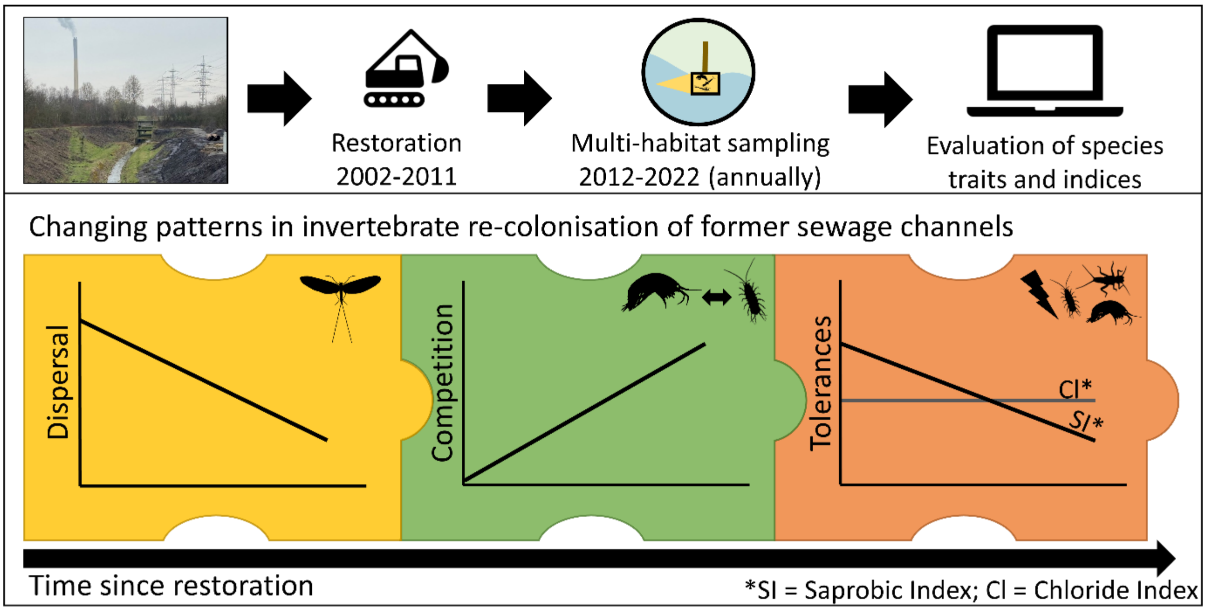

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# How tolerances, competition and dispersal shape benthic invertebrate colonisation in restored urban streams

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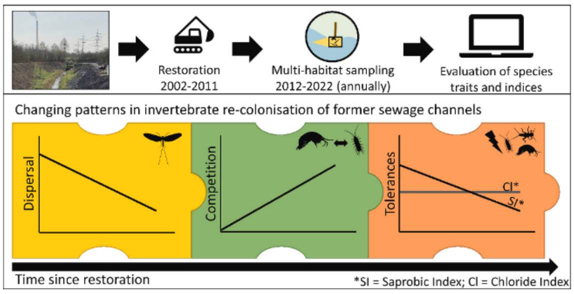
## HIGHLIGHTS

- We investigated benthic invertebrate recolonisation of urban streams over 11 years.
- Dispersal capacity drives community assembly in the initial phase of colonisation.
- Interspecific competition increases over time as habitats and communities mature.
- Species' organic pollution tolerance is relevant during the recolonisation process.

## GRAPHICAL ABSTRACT



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## ABSTRACT

Biotic communities often respond poorly to river restoration activities and the drivers of community recovery after restoration are not fully understood. According to the Asymmetric Response Concept (ARC), dispersal capacity, species tolerances to stressors, and biotic interactions are three key drivers influencing community recovery of restored streams. However, the ARC remains to be tested. Here we used a dataset on benthic invertebrate communities of eleven restored stream sections in a former open sewer system that were sampled yearly over a period of eleven years. We applied four indices that reflect tolerance against chloride and organic pollution, the community's dispersal capacity and strength of competition to the benthic invertebrate taxa lists of each year and site. Subsequently, we used generalised linear mixed models to analyse the change of these indices over time since restoration. Dispersal capacity was high directly after restoration but continuously decreased over time. The initial communities thus consisted of good dispersers and were later joined by more slowly dispersing taxa. The tolerance to organic pollution also decreased over time, reflecting continuous improvement of water quality and an associated increase of sensitive species. On the contrary, chloride tolerances did not change, which could indicate a stable chloride level throughout the sampling period. Lastly, competition within the communities, reflected by interspecific trait niche overlap, increased with time since restoration. We show

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that recovery follows a specific pattern that is comparable between sites. Benthic communities change from tolerant, fast dispersing generalists to more sensitive, slowly dispersing specialists exposed to stronger competition. Our results lay support to the ARC (increasing role of competition, decreasing role of dispersal) but also underline that certain tolerances may still shape communities a decade after restoration. Disentangling the drivers of macroinvertebrate colonisation can help managers to better understand recovery trajectories and to define more realistic restoration targets.

## 1. Introduction

Water managers apply a wide range of restoration measures to convert degraded into more natural streams (Feld et al., 2011; Palmer and Ruhí, 2019). Often, these measures focus on hydromorphological improvements and the increase of local habitat diversity (Frainer et al., 2018; Lorenz et al., 2009). In response to these efforts, communities of aquatic biota including sensitive species are expected to colonise the restored streams. However, reality frequently diverges from this "field of dreams" hypothesis (if we build it, they will come; Palmer et al., 1997): biota often respond weakly, if at all, to restoration activities (Louhi et al., 2011; Omoniyi et al., 2022; Palmer et al., 2010).

To understand this unexpectedly weak response of biota, we need to identify the filters that influence the (re)assembly of aquatic communities in restored streams, and their changing role over time. Depending on the measures, restoration may improve water quality, e.g. by eliminating sources of pollution which decreases nutrient levels, and/or create and diversify bottom habitats (Frainer et al., 2018). For instance, re-meandering or re-braiding a river reach increases habitat diversity by amplifying flow complexity (Lorenz et al., 2009), subsequently enhancing substrate diversity and oxygen availability. Planting woody riparian vegetation, or improving the conditions for its growth, causes dead leaves and woody debris to fall into the river, thus providing organic microhabitats and food for shredders among the benthic invertebrates. Riparian vegetation is also shading the stream, thereby cooling the water and providing niches for cold-stenothermic species (Davies-Colley et al., 2009; Thompson and Parkinson, 2011). All these measures thus modify and increase the available niches for aquatic organisms, by providing habitats and by improving water quality (Gillmann et al., 2023).

Not all benthic invertebrate species can colonise these new niches. Possible colonisers are restricted by their dispersal capacity and by the distance of source populations of the restored site (Sundermann et al., 2011). For a species to colonise a new site, it must be within its range of dispersal capacity (Li et al., 2016) and the environmental conditions have to meet the species' tolerance range. After the species' arrival at the site, interspecific biotic interactions such as competition for food and space govern community assembly (Lake et al., 2007). These three filters controlling the recolonisation process can thus be summarised as dispersal, tolerances and competition.

Species differ in their dispersal capacities. Species with a flying adult stage (merolimnic) can disperse faster and across longer distances (Peredo Arce et al., 2021, 2023), while hololimnic species spend their whole life cycle in the water and can only disperse via drift, active swimming or phoresy (Li et al., 2016). The presence of and distance to population sources filters the species available to colonise a new (restored) stream reach (Sundermann et al., 2011). Barriers can additionally prevent species from reaching other stream sections, e.g. dams or urban areas (Brederveld et al., 2011). Consequently, the order in which restored stream sections are colonised is highly context specific and depends on the species' dispersal capacity, source populations and the connectivity of the stream network (Peredo Arce et al., 2023; Sarremejane et al., 2017; Tonkin et al., 2014). A pioneer community at a freshly restored site is therefore supposed to mainly consist of fast dispersers, thus active flying species. However, over time, more slowly dispersing species arrive and the importance of dispersal capacity for community assembly decreases.

Successful establishment of a species depends strongly on the environmental conditions provided by the restored site (Alves et al., 2020). Every species has a certain niche space, which defines the range of environmental conditions, and habitat requirements that are most favourable and the borders in which it can survive (Soberon and Peterson, 2005). Tolerant and sensitive species differ in their niche width, which is either wide or narrow, respectively (Heino and de Mendoza, 2016). The changing conditions following restoration in combination with the tolerance of members of the local species pool are thus important for community assembly. This filter, however, is especially relevant in degraded and polluted streams, in which only tolerant species can settle and survive (Feld and Hering, 2007). After restoration, with the improvement of water quality, the relevance of tolerances is expected to decrease, as the conditions are increasingly suitable for both, sensitive and tolerant species. Tolerances of benthic invertebrate species to various stressors are available through species-trait databases (Schmidt-Kloiber and Hering, 2015).

The niche of a species does not only include its tolerance ranges. Other important aspects are bottom substrates, flow velocity and food that jointly define habitat requirements (Soberon and Peterson, 2005). Once a habitat has been colonised by the first settling species, new arriving species with similar habitat requirements have to compete for food and space (Vanni et al., 2009). The degree of competition depends on the availability of resources and the number of species and individuals. Thus, during colonisation, competition is expected to increase over time because more species with similar habitat and food preferences, i.e. traits, arrive. A patch already occupied by an early arriving species is more difficult to occupy for late arrivers (Eglesfield et al., 2023; White et al., 2021). Although in some cases species with similar preferences can coexist, either by sharing the habitat and food source or by adapting to a less favourable niche (Leibold and McPeek, 2006), the importance of biotic interactions in community assembly is expected to increase as more species arrive, i.e. with time since restoration.

Vos et al. (2023) recently published the "Asymmetric Response Concept" (ARC) that relates the relevance of these three filters – dispersal, tolerance and biotic interactions – to different phases of degradation and recovery. According to the ARC, the relevance of tolerance will decline sharply with restoration, due to the release of stressor impact and the corresponding change of environmental conditions. The role of dispersal will sharply increase, and be particularly relevant in the first phase after restoration, while newly established niches are filled. Subsequently, the role of biotic interactions will increase, which will be of prime importance in mature restored rivers, since the established species have to compete with an increasing number of newly arriving species.

Restored urban streams and their benthic invertebrate communities are a well-suited testing ground for processes of community recovery. Compared to other stream categories, they have faced a dramatic loss of biodiversity caused by various anthropogenic impacts. For example, channelization drastically increases discharge and consequently, erosion decreases habitat quality and quantity (Brooker, 1985). In addition, water quality suffers from rainwater runoff and the input of wastewater, which increases salinity and decreases oxygen availability (Barałkiewicz et al., 2014). Benthic invertebrates respond particularly sensitive to environmental changes, e.g. to pollutant input, and act as indicators for water quality in water bodies (Al-Zankana et al., 2020). The remnant community is therefore often very simple, and recolonisation sources are sparse. In extreme cases, the pre-restoration community is almost depleted, as the streams were heavily polluted before restoration. Accordingly, competition patterns may remain simple, even over longer time spans after restoration.

In this study, we used long-term monitoring data of a restored urban stream catchment, the Boye in West Germany that comprises eleven consecutive years of benthic community data. The Boye system was used as an open sewer until the 1990s. Therefore, only a few tolerant species survived. A previous study using a subset of the data showed that changes in the benthic community over time are closely linked to changes in habitat and water quality conditions such as a decrease in conductivity (Gillmann et al., 2023). Here we used this long-term dataset to test the ARC. Based on the original hypotheses formulated by Vos et al. (2023), we investigated the following hypotheses:

1. (1) Following stream restoration, dispersal becomes the primary driver for colonisation in the initial recolonisation phase. Species with high dispersal capacities quickly occupy the unoccupied ecological niches.
2. (2) Over time, species with lower dispersal capacities gradually populate the restored sites. With the growing number of species, we expect a corresponding increase in trait overlap, leading to an increase in competition.
3. (3) We assumed that the stressors shaping the communities were eliminated during the restoration process. Therefore, we expect that species tolerances will play a minor role in the process of community recovery.

Our study is the first to test the concept of the ARC. We addressed a restored urban stream catchment using long-term monitoring data to improve our understanding of the mechanisms driving the (re)assembly of benthic invertebrate communities over time and inform more effective restoration strategies.

## 2. Material and methods

### 2.1. Study area and study sites

The Boye catchment is located in Western Germany within the Ruhr Metropolitan Area, which is one of the largest urban agglomerations in Europe with about 5.3 million inhabitants. The Boye is a tributary to the larger Emscher River, which flows into the Rhine River. The Boye catchment drains an area of 77 km$^2$ and has a total stream length, including the tributaries, of 90 km (Fig. 1). Almost all streams in the catchment are sandy lowland streams (stream type 14 according to Pottgiesser and Sommerhäuser, 2014). The downstream sections of the Boye and its larger tributaries pass through highly urbanised areas, while agricultural land and forests predominantly surround the upstream sections (Fig. 1). The Boye stream network, except for a few upstream sections, was used as an open sewer in the twentieth century until wastewater was removed from most sections in 2007 and 2009 (Table 1). Meanwhile, the Emscher continued to carry wastewater until the end of 2022, serving as a barrier for dispersal of Neobiota from downstream areas.

The hydromorphological restoration of several tributaries was

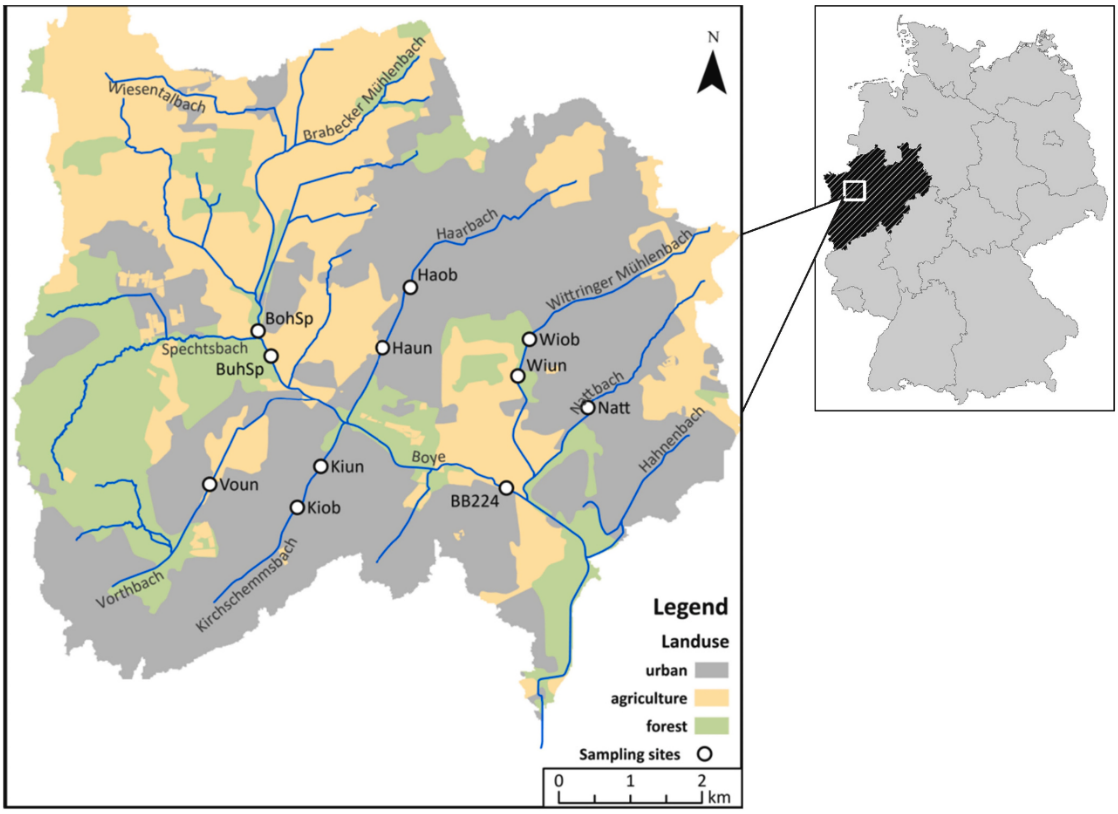

**Fig. 1.** Map of the Boye catchment (Ruhr Metropolitan Area, Western Germany) with the sampling sites (dots). Three major types of landuse of the catchment (merged from CORINE and InVeKos) are displayed in different colours: urban (grey), agriculture (yellow), forest (green).

**Table 1**
List of sampling sites.

| Stream name | Site ID | Coordinates | Wastewater-free since | Hydromorphological restoration |
|---|---|---|---|---|
| Boye | BB224 | 51.54505°N<br>6.982227°E | 2017 | 2019 |
| Boye | BohSp | 51.56429°N<br>6.930277°E | 2007 | 2002 |
| Boye | BuhSp | 51.56120°N<br>6.933041°E | 2007 | 2002 |
| Haarbach | Haun | 51.56279°N<br>6.956702°E | 2009 | 2010 |
| Haarbach | Haob | 51.570724°N<br>6.960792°E | 2009 | 2010 |
| Kirchschemmsbach | Kiun | 51.548051°N 6.943958°E | 2007 | 2007 |
| Kirchschemmsbach | Kiob | 51.541859°N<br>6.939128°E | 2007 | 2007 |
| Nattbach | Natt | 51.557192°N 6.999138°E | 2009 | 2011 |
| Vorthbach | Voun | 51.544019°N<br>6.921747°E | 2007 | 2011 |
| Wittringer | Wiun | 51.560245°N 6.98305°E | 2009 | 2010 |
| Wittringer | Wiob | 51.564035°N<br>6.986361°E | 2009 | 2010 |

finished by the year 2011. Measures included the removal of concrete bed and bank reinforcements, streambed widening and a transformation to sinuate or semi-meandering channels. Starting in 2012, selected sites at the restored stream sections were subjected to a monitoring of benthic invertebrate recolonisation for eleven consecutive years (see also: Gillmann et al., 2023; Winking et al., 2014, 2016). In this study, we used data from eleven of these restored sites (Table 1), located in the urbanised part of the catchment. The average conductivity of the sites decreased over time, from 1597 µs/cm to 924 µs/cm. Sites that were proven to be intermittent during the investigation period were excluded, because their colonisation patterns presumably differ from those of permanent streams. At the time our sampling started, the individual streams were in different phases of development (Table 1): some were already hydromorphologically restored several years ago (e.g. BohSp, BuhSp), while others were freshly restored (e.g. Natt) and a single site was restored later (BB224) - in this case, the sampling commenced in year 5 of the study, once the site was wastewater-free.

### 2.2. *Sampling, sorting and identification*

At the selected sites, standardised multi-habitat sampling (Haase et al., 2004) was carried out annually in March or April from 2012 to 2022. The method involves estimating the proportions of the bottom substrate in a 50 m long reach that is representative for a longer stream section. Substrates were assessed in 5 % steps and subsequently sampled with one sampling unit (25 × 25 cm) per 5 % habitat coverage, resulting in 20 sampling units per site. We pooled the samples and preserved them in ethanol (96 %). Subsequently, the samples were sorted and identified in the laboratory (Meier et al., 2006). We identified the species to the lowest taxonomic level possible, adhering to the operational taxa list for Germany (Haase et al., 2006). Accordingly, most organisms were identified to species level, except Chironomidae (tribe level), Diptera (family level) and Oligochaeta (family level). Species counts were standardised based on abundance (measured as individuals/m$^2$). Prior to the analysis, adjustments were made to the taxalist to accommodate the varying levels of identification of different larval instars (Nijboer and Schmidt-Kloiber, 2004).

### 2.3. *Data analysis*

The analysis addressed the three major filters supposed to influence colonisation patterns. For each filter, we selected traits that we subsequently used for an index to analyse the change of the corresponding factor over time. We collected data on respective traits for all taxa that were found since 2012.

#### 2.3.1. *Dispersal*

We selected dispersal classes defined by Winking et al. (2014) (Table 2) because this index combines two important metrics to describe a species' colonisation potential, the dispersal capacity and niche breadth (degree of specialisation). In addition, it operates exactly on the taxonomic resolution level (mainly species) we applied in our study. Based on literature and expert knowledge, the authors defined five classes that reflect a species' dispersal capacity. Criteria include the ability to fly (merolimnic vs. hololimnic taxa), the aerial dispersal capacity and the degree of habitat specialisation, i.e. assuming that habitat generalists (r-strategists) are generally stronger dispersers as compared to habitat specialists (Li et al., 2021). One of the classes is limited to hololimnic taxa that exclusively disperse in their aquatic life stages. Taxa not covered by Winking et al. (2014) were assigned to a class based on a similar procedure, resulting in a coverage of 83 % of all present taxa. Of the remaining 17 %, 14 % were only identified to higher taxonomic levels, which did not allow a classification, and for 3 % not enough information was available to define a class for the species.

The classes that originally spanned from A to E were recalibrated by ranking the dispersal capacity from 1 to 5, with class 5 describing the fastest and strongest colonisers (high aerial dispersal capacity, habitat generalists) and class 1 describing the slowest colonisers (exclusively aquatic dispersal) (Table 2). This recalibration allowed us to calculate an index from the mean of these classes based on the occurring species. The resulting values were finally converted into a comprehensive index spanning from 0 to 1, where 1 describes a community exclusively composed of strong dispersers. This index will be referred to as Dispersal Index in the following.

#### 2.3.2. *Competition*

We selected three traits that are considered to play a major role for competition processes: feeding type (assuming a competition for food),

**Table 2**
Dispersal classes defined by Winking et al. (2014). Class rankings are defined in the order of dispersal capacity.

| Class | Class ranking | Definition |
|---|---|---|
| A | 1 | Aquatic dispersal |
| B | 2 | Low aerial dispersal, habitat specialist |
| C | 4 | High aerial dispersal, habitat specialist |
| D | 3 | Low aerial dispersal, habitat generalist |
| E | 5 | High aerial dispersal, habitat generalist |

habitat preference (assuming a competition for space on the microscale) and stream zonation preference (i.e. the preferences for species in the longitudinal space of a river; assuming a competition for space on the macroscale). We downloaded the trait values from the database freshwaterecology.info (Schmidt-Kloiber and Hering, 2015). Each of the traits had a good coverage across taxa with 95 % for feeding type, 87 % for habitat preference and 74 % for stream zonation preference. In the database, the traits of each species are defined in a 10-point system, where different affinities are assigned to a range of trait properties (fuzzy coded). We defined competition as the proportion of trait overlap between species. A high trait overlap means that two species favour similar habitat conditions and food sources. Therefore, they compete for the same resources. We used the Gower Similarity from the "gawdis" package in R (v.0.1.5, de Bello et al., 2021) to analyse the trait overlap. The Gower distance determines the similarity between traits of species. The "gawdis" function allows to group different trait properties that describe a single trait, based on which an overall Gower distance is calculated. A low distance, thus high similarity, between species traits depicts a high likelihood of competition between species. We calculated the trait similarity between taxa pairs of the individual taxalists per sampling site and year. Finally, we summarised the values as the mean Gower Similarity per site and year.

#### 2.3.3. Tolerances

We used two indices that targeted tolerances against organic pollution and salinization. As the streams were formerly heavily polluted, only taxa with a strong tolerance against organic pollution could occur, a lasting impact that may affect the recolonisation process. Chloride is a common stressor in sewage-polluted waters and remains to be problematic even after wastewater was removed (Pereda et al., 2020). Previous studies revealed a high conductivity in the Boye system (Gillmann et al., 2023; Winking et al., 2014, 2016), a legacy of mining and a consequence of urbanisation. Consequently, high salinity concentrations are likely to strongly impact benthic invertebrates (Kefford et al., 2016).

The German Saprobic Index (GSI) was selected to indicate the tolerance of the benthic community against organic pollution. The Index is originally used to determine the water quality of streams (Kolkwitz and Marsson, 1909). A high Saprobic Index (SI) translates into high organic pollution. The Index is derived from the saprobic values of a species, its indicator weight and abundance (Zahradkova and Soldan, 2013). We downloaded the saprobic values for Germany from freshwaterecology.info (Schmidt-Kloiber and Hering, 2015). They were available for 43 % of all taxa. Despite its relatively low coverage across taxa, we used this Index because it is commonly applied to assess organic pollution based on the assigned taxa. Furthermore, not all taxa exhibit a preference for a certain saprobic condition. We used the standard formula to calculate the German Saprobic Index, however, instead of abundance, we only included species presence-absence values to gain comparability with the other indices used in this study. We refer to this modified index as Saprobic Index in the following.

We collected chloride tolerances of the species from Verberk et al. (2012), which is based on tolerances derived from a literature analysis and coded in a ten-point system. The database covered 78 % of the taxa investigated in this study. We translated this system into a Chloride Index ranging from 0 to 1, using the same method and formula as used for the Saprobic Index. A high value depicts a high chloride tolerance of the community.

#### 2.3.4. Statistics

We used the indices to address our hypotheses concerning changes of the role of dispersal, competition and tolerances with time since restoration. The species' traits and indices were not correlated with each other, which was tested using the "cor" function (package "stats", v.4.1.2, R core Team, 2021). The indices served as response variables for generalised linear mixed models (GLMM) with beta error distribution (package "glmmTMB", v.1.1.8, Brooks et al., 2017). We used a beta distribution with a logit link function because all response variables lay between 0 and 1. Time since restoration [years] was used as a fixed effect. The streams and sites were included as random effects, with sites nested under the streams, to account for the variance component between streams and sites. The conditional R-squared was calculated by correlating the fitted with the predicted values. The residuals were visualised in QQ-plots (package "DHARMa", v.0.4.6, Hartig and Lohse, 2022), which are attached in Appendix A. Our tests for spatial autocorrelation, for which we used the "testSpatialAutocorrelation" function (package "DHARMa", v.0.4.6, Hartig and Lohse, 2022) were non-significant. Further, including a spatial autocorrelation structure in our models led to overfitting. The test outputs can be found in Appendix B.

The data was analysed in Rstudio (v.4.1.2) and visualised using the package ggplot2 (v.3.4.1, Wickham, 2016).

## 3. Results

In the 116 samples (11 sites; 10 of which were sampled over 11 years and one over 6 years) we found 143,283 individuals of 175 taxa. Taxa numbers ranged from 2 to 41 (median 23), abundance from 99.2 Ind/m$^2$ to 6406 Ind/m$^2$ (median 1030 Ind/m$^2$). The most frequent taxa were Limnephilini gen. sp., Chironomidae gen. sp., Tanypodinae gen. sp. The most dominant taxa were Chironomidae gen. sp. and *Gammarus pulex*.

### 3.1. Dispersal

The Dispersal Index was largest in the freshly restored streams. With time since restoration, the Dispersal Index decreases (Fig. 2). In the first two years that are shown in Fig. 2 (−1 and 0), there is one site in which the Dispersal Index increases at first (BB224). However, the first sample taken here included only two taxa. The lower end of the graph (16–20 years after restoration) displays the lowest Dispersal Index for the two sites in the catchment that were restored first. Over all sampling sites the GLMM captures 46 % of the variance in the data ($R^2 = 0.46$). The regression coefficient is significantly different from zero, $p < 0.001$ (mean = −0.04, 2.5 % = 0.3, 97.5 % = 1.01).

### 3.2. Competition

The Gower Similarity Index increases by 10 % within 11 years after restoration, indicating a slightly increased trait overlap within the communities (Fig. 3). An increase in Gower Similarity was observed at almost all sites and across the whole observation period. The sites within two streams displayed a decrease in similarity within the first few years after restoration, before it increased for the remaining sampling period (streams "Haarbach", "Wittringer"). The community with the lowest similarity was observed four years after restoration ("Wiun") with <35 % similarity. This site also showed the strongest increase in similarity, reaching 50 % after ten years. A similar increase in Gower Similarity was observed at another site ("Haob"). In contrast, little change was observed at the sites in the Kirchschemmsbach ("Kiob", "Kiun"), which were restored a few years before most of the other sites (Table 1). The first sample of BB224 (TsR: −2 years) was excluded because the Index could not be calculated for two taxa. The model captures 37 % of the variance in the data ($R^2 = 0.37$). The regression coefficient is significantly different from zero $p < 0.001$ (mean = 0.01, 2.5 % = −0.27, 97.5 % – 0.03).

### 3.3. Tolerances

The Saprobic Index (standardised to values between 0 and 1) decreases with time since restoration (Fig. 4). This trend was similar among all sampling sites. The highest Saprobic Index of close to 0.65 was observed three years after restoration ("Natt"), while the lowest Saprobic Index of 0.4 was found eight years after restoration ("Wiob"). The

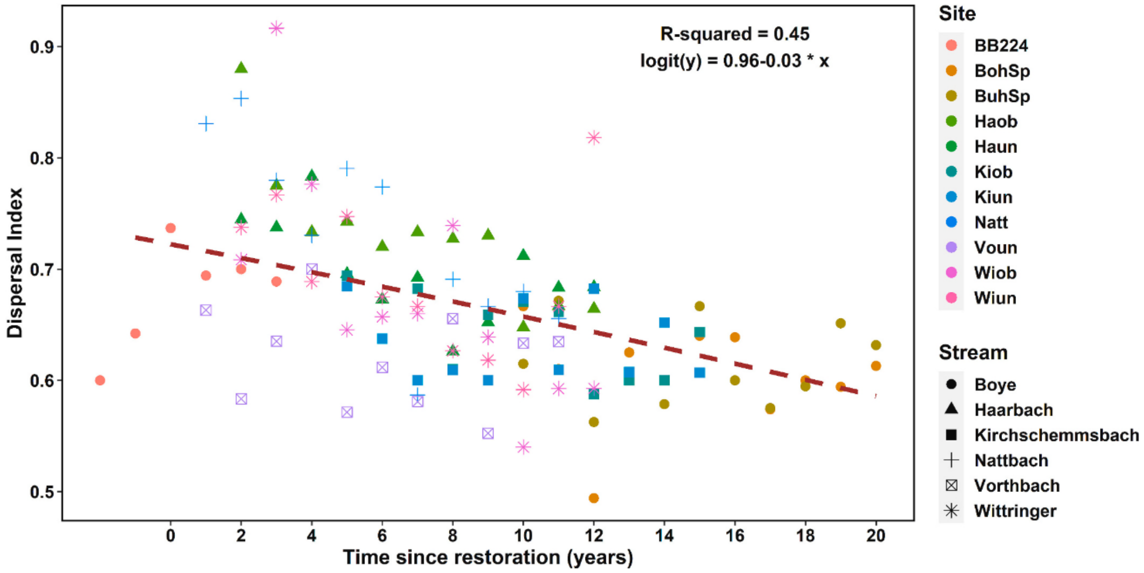

**Fig. 2.** GLMM of the communities' Dispersal Index (mean dispersal classes) over time since restoration. The classes are a combination of the species' dispersal capacity and habitat specialisation. A logit link function was used. Streams and sites were included as random effects. Each sample is represented by one dot.

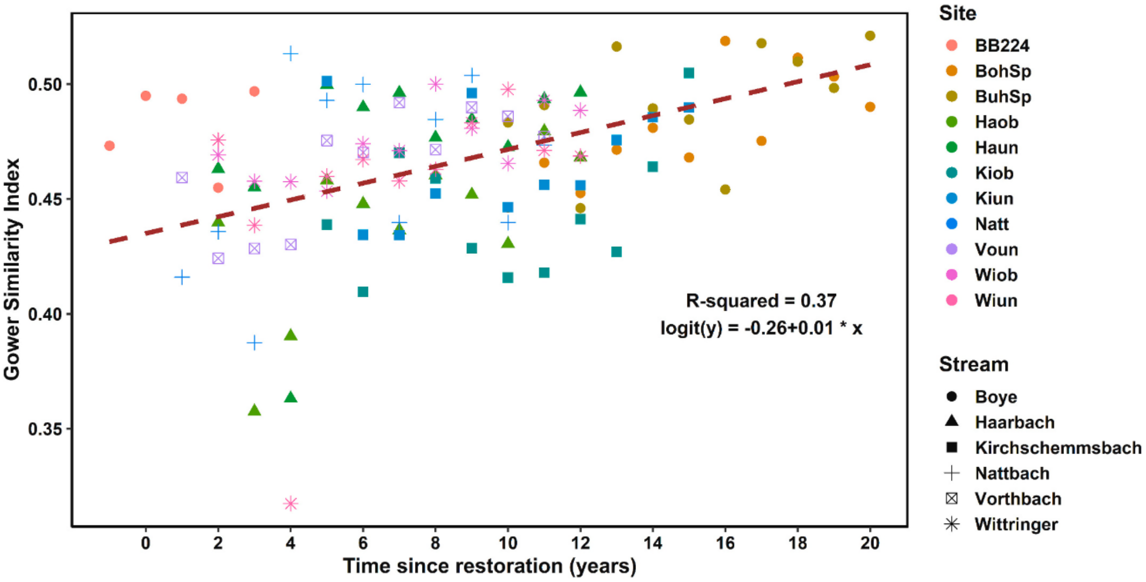

**Fig. 3.** GLMM of the Gower Similarity Index, representing the overlap between species traits (proxy for competition). A logit link function was used. Streams and sites were included as random effects. Each sample is represented by one dot.

model captures 43 % of the variance in the data ($R^2 = 0.43$). The regression coefficient is significantly different from zero $p < 0.001$ (mean = −0.02, 2.5 % = −0.04, 97.5 % = 0.34).

The Chloride Index (chloride tolerance) remained stable over time, showing only a slight increase toward the end, however, the range in which changes were observed is not higher than 0.01 (Fig. 5). The model captures 2 % of the variance in the data ($R^2 = 0.02$). The regression coefficient is not significantly different from zero $p > 0.001$ (mean = 0.01, 2.5 % = −4.94, 97.5 % = −4.7).

## 4. Discussion

Our study is the first comprehensive test of the Asymmetric Response Concept (ARC, Vos et al., 2023) which outlines a predictable change of the drivers of community recovery with time since restoration: The role of dispersal is expected to be most relevant directly after restoration and

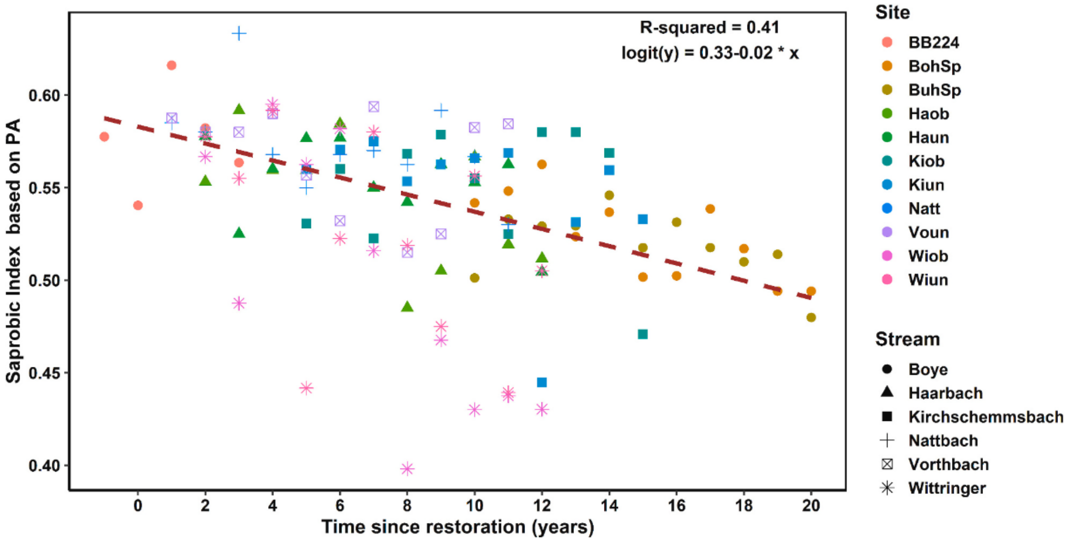

**Fig. 4.** GLMM of the Saprobic Index based on species presence/ absence. A logit link function was used. Streams and sites were included as random effects. Each sample is represented by one dot.

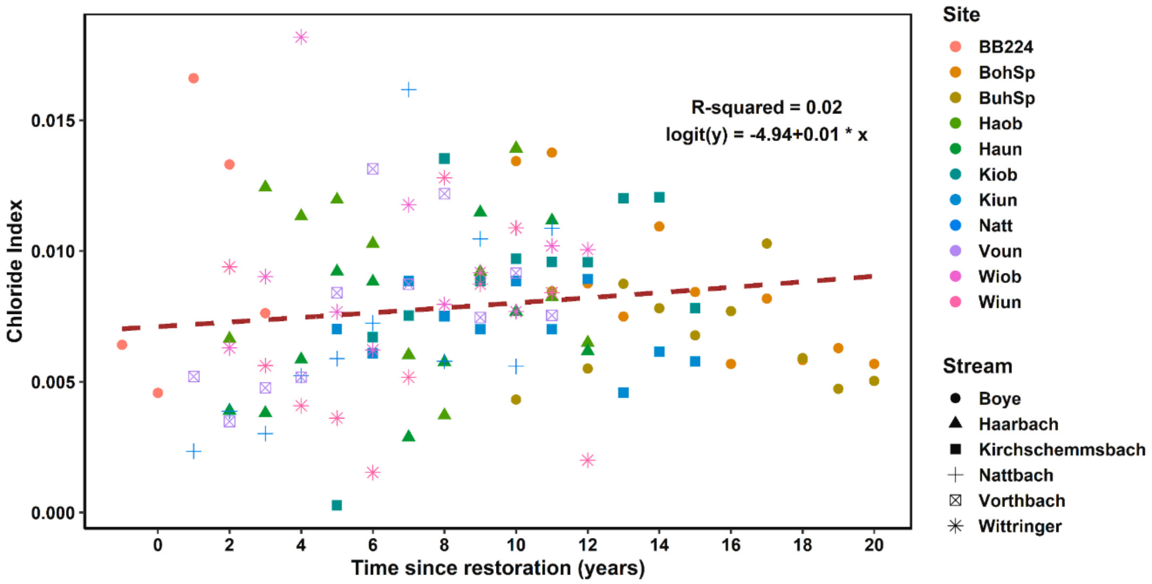

**Fig. 5.** GLMM of the Chloride Index (chloride tolerance). A logit link function was used. Streams and sites were included as random effects. Each sample is represented by one dot.

to decline afterwards, the role of tolerance against stressors is expected to decline sharply with restoration and to stay on low levels afterwards, while the role of biotic interactions (here: competition) is expected to increase. These general patterns were supported by our results, albeit with some modifications.

### *4.1. Dispersal*

We hypothesised that initial colonisation is mainly performed by good dispersing species. Indeed, the communities with the largest Dispersal Index were present during the first three years after restoration. This means a large proportion of the taxa in these communities belong to the group with a high aerial dispersal capacity and with a low degree of habitat specialisation (class E as defined by Winking et al., 2014). Benthic invertebrate species with a high aerial dispersal capacity have the best chance to quickly disperse over great distances and habitat generalists have best options to find suitable habitats (Grönroos et al., 2013). Already in a previous study (Gillmann et al., 2023), we found the streams to be first colonised by the good dispersing species *Cloeon dipterum* (Ephemeroptera) and different Coleopteran species. A similar pattern was observed by Winking et al. (2014, 2016) in the same catchment, albeit limited to the first few years of recolonisation and by Lorenz (2020) in a more natural setting. Once habitat specialists arrive, which are often also weaker dispersers, they can outcompete the generalists in their preferred habitat (Verberk et al., 2010). Therefore, the Dispersal Index decreases over time, as good dispersing habitat generalists are replaced by weak dispersing habitat specialists. These weak dispersing habitat specialists are expected to be the main inhabitants of headwater streams with strong species sorting (Li et al., 2018). However, since they take more time to establish a population in a new habitat, they can only be dominant in mature streams. Generally, dispersal is considered to play a greater role for community assembly in larger downstream sections, which receive significant dispersal inputs due to their central position (Brown and Swan, 2010; Cathey and Brown, 2022).

Aquatic dispersal can be slower than aerial dispersal as the species are restricted to the stream corridors (Li et al., 2016). However, the presence of an undisturbed area upstream of a disturbed site facilitates faster recolonisation, most likely through drifting organisms (Winking et al., 2014). Studies have shown that hololimnic species can form part of the pioneer community (Cañedo-Argüelles and Rieradeval, 2011; Gillmann et al., 2023). If upstream colonisation sources are missing, it is most likely that the species were present prior to restoration and were able to prevail under the previous degraded conditions or that they recolonised through phoresy (Eglesfield et al., 2023).

While we demonstrated that dispersal capacity is a strong filter in the early phase after restoration, dispersal is not only influenced by the species' traits. The species' presence and especially the rate of its occurrence in nearby population sources is crucial for colonisation (Sundermann et al., 2011; Tonkin et al., 2014). In addition, barriers can hinder them from reaching new habitats, despite the presence of nearby source populations (Bond and Lake, 2003; Lake et al., 2007). Such dispersal constraints are commonly observed in urban or agricultural areas because restored streams are mostly disconnected or too far away from natural sections. The streams connectivity is therefore another important factor for successful colonisation (Brown et al., 2018). In the initial phase of the Boye recolonisation, this pattern was observed as well: the first streams that were colonised, especially with hololimnic organisms, were those with an upper stream section that was never used as an open sewer (Winking et al., 2014).

### 4.2. *Competition*

Our results underline the foremost importance of dispersal for benthic invertebrate colonisation of new habitats. They further demonstrate that as soon as the pioneer community is joined by more specialised species, competition for food sources and suitable microhabitats starts to play a potential role for community assembly (Eglesfield et al., 2023; Mackay, 1992). We hypothesised that competition increases over time as species numbers increase. We selected the Gower Similarity Index as a measure for competition, which displays the amount of trait overlap between species regarding habitat and food preferences. Our hypothesis was supported, since the overall Gower Similarity increases over time, albeit not from the start. In the first few years after restoration, the similarity even decreases (e.g. streams "Haarbach", "Wittringer"). This observation is limited to communities that were sampled early after restoration. In the year with the lowest Gower Similarity, less than eleven taxa were found at two sampling sites ("Haob" and "Wiun"). However, the number of taxa was greater in the first two sampling years. The first arriving species were generalists, as shown by the Dispersal Index. Therefore, they had similar preferences, resulting in a high Gower Similarity. New habitats, supported, e.g. by riparian vegetation growth need time to develop (Ward et al., 2002). As more habitats developed and more species with different preferences arrived, the similarity decreased at first and started to increase again afterward. The initial decrease displays the ongoing change in habitats shown in our previous study (Gillmann et al., 2023). Stream restoration disrupts the streams ecosystem. Depending on the dimension of the restoration project, stream water was redirected from the reaches that are to be restored. Once the restored streambed was re-watered, the new ecosystem started to develop. While the initial habitats typically consisted of sludge, the habitat diversity increased as the streams matured. Natural succession of the riparian vegetation leads to the development of new habitats, which leads to an increase in species diversity of benthic invertebrates (Gillmann et al., 2023; Haase et al., 2013; Verdonschot et al., 2016). Only after more stable habitats have developed, a community establishes that is governed by biotic interactions (White et al., 2021).

Few sites, for which sampling started several years after the end of restoration, showed only minor increases in Gower Similarity ("Kiob", "Kiun", "BohSp" and "BuhSp"). These communities already had time to establish stable habitats and associated communities with similar habitat and food preferences (Little and Altermatt, 2018). Similarly, Archaimbault et al. (2005) and Charvet et al. (2000) identified high stability of biological and ecological traits in settled reference sites.

### 4.3. *Tolerances*

Next to habitat and food sources, stressors such as organic pollution can determine community development (Nguyen et al., 2023). The ARC describes tolerances to be the major determinant of community assembly during the stressor phase, i.e. prior to restoration (Vos et al., 2023). The major stressors are expected to be eliminated during the restoration process and should therefore not interfere with the recolonisation process. However, many restoration projects focus on morphological restoration, while other stressors responsible for community degradation are not addressed (Brettschneider et al., 2023).

We tested the hypothesis that tolerances would play a minor role for the colonisation process of restored sites by investigating changes in the communities' Chloride and Saprobic Indices. Previous studies of the Boye system revealed high conductivity values for several of the study sites (Gillmann et al., 2023; Winking et al., 2016). High conductivity values are associated with elevated salinity, caused e.g. by chloride input (Kaczmarek et al., 2023). During the first few years after restoration, conductivity was observed to decrease (Gillmann et al., 2023). We therefore expected the Chloride Index to decrease over time, meaning an increase in chloride sensitive species. However, the chloride tolerance did not change. Chloride was found to be a major determinant of macroinvertebrate richness in previous studies (Bekele et al., 2021). A missing response of the community could therefore demonstrate that chloride values remained stable over time. For all species, we identified the chloride tolerance to be at the lower end of the Index. Thus, all species occurring in the Boye catchment are equally tolerant to the existing chloride conditions. High conductivity is caused by an increase in dissolved ions. Hence, the high conductivity in the Boye catchment could have been caused by other ions than chloride (Kefford et al., 2016).

Against our expectation, the Saprobic Index, modified by using only presence and absence, decreased with time since restoration at most sites. Urbanisation and wastewater input cause high organic enrichment and eutrophication in streams (Brabec et al., 2004). The decrease of the Saprobic Index demonstrates an improvement in water quality and proofs that the streams are still recovering. Jesus and Monteiro (2022), who investigated the recovery of an urbanised stream in Portugal, found a similar effect. They identified a larger proportion of taxa sensitive to pollution (e.g. EPT) not before the 5th year of recovery. In addition, in case of the Boye catchment, the species present in the initial phase of community development were those that could survive under the heavily polluted previous conditions and it took time until more sensitive species arrived (Gillmann et al., 2023). Some tolerant species can inhibit the arrival of more sensitive species, e.g. by niche pre-emption (Eglesfield et al., 2023). High Saprobic Indices may therefore not reflect the degree of organic pollution but simply dispersal constraints. Once the more sensitive species have arrived, we expect the Saprobic Index to remain stable.

The lowest Saprobic Index, thus most sensitive species, was found at "Wiob", eight years after restoration. However, at the same site, the Saprobic Index increases again afterwards. This could have been caused by the severe drought that Germany experienced in 2018. Low water levels coupled with eutrophication and organic enrichment may have caused the loss of sensitive species and consequently an increase of the Saprobic Index.

## 5. Conclusion

Understanding the recolonisation patterns that act while new communities are forming in restored stream sites is crucial to inform stream managers and further improve restoration measures. In many cases, the biotic response to restoration remains minor, if there is any at all. Our results identify dispersal capacity coupled with the amount of habitat specificity of species as the main initial driver for community development. It is therefore important that the restored sections are connected to source populations to not constrain this process. Only then, more species can arrive at the restored site, which will initialise competition. If the environmental conditions are favourable, habitat specialists can outcompete generalists. Species tolerances may continue to play a role in this process, if restoration measures did not fully release environmental stressors. The colonisation pattern was mostly reproducible across our studied sites and gives first evidence for the assumptions of the ARC. Future investigations should address whether the patterns are similar in other catchments, especially with different landuse and proximity to more natural sites, and with a more species-rich initial community that may pose much more resistance to recolonisation from the very beginning.

## CRediT authorship contribution statement

**Svenja M. Gillmann:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **Armin W. Lorenz:** Writing – review & editing, Supervision, Methodology, Data curation, Conceptualization. **Willem Kaijser:** Writing – review & editing, Formal analysis. **Hong Hanh Nguyen:** Writing – review & editing, Formal analysis. **Peter Haase:** Writing – review & editing. **Daniel Hering:** Writing – review & editing, Supervision, Methodology, Conceptualization.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

Data will be made available on request.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2024.172665.

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## Supplementary Materials

### Appendix A: QQ-plots to visualise the residuals of the GLMMs per Index

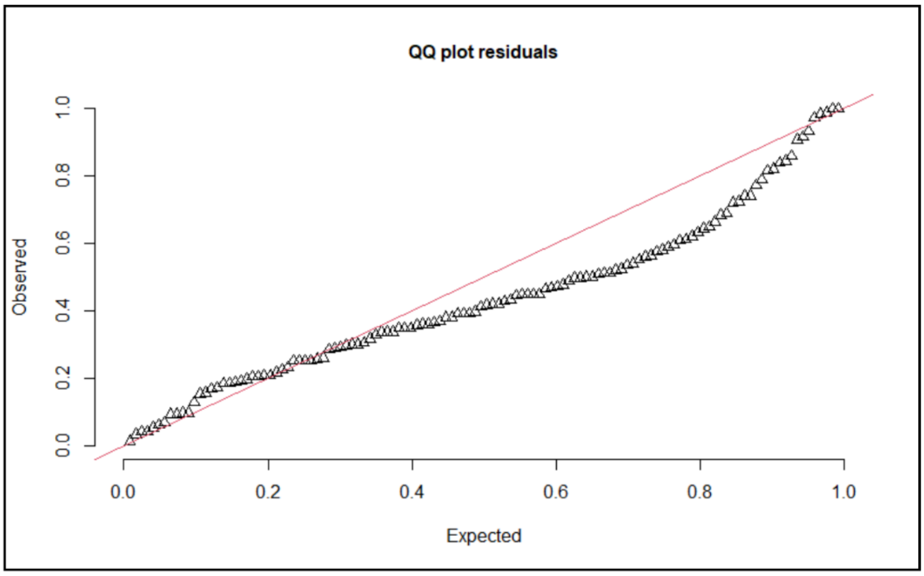

Figure A.1: QQ-plot of GLMM using the Dispersal Index as response and time since restoration as predictor.

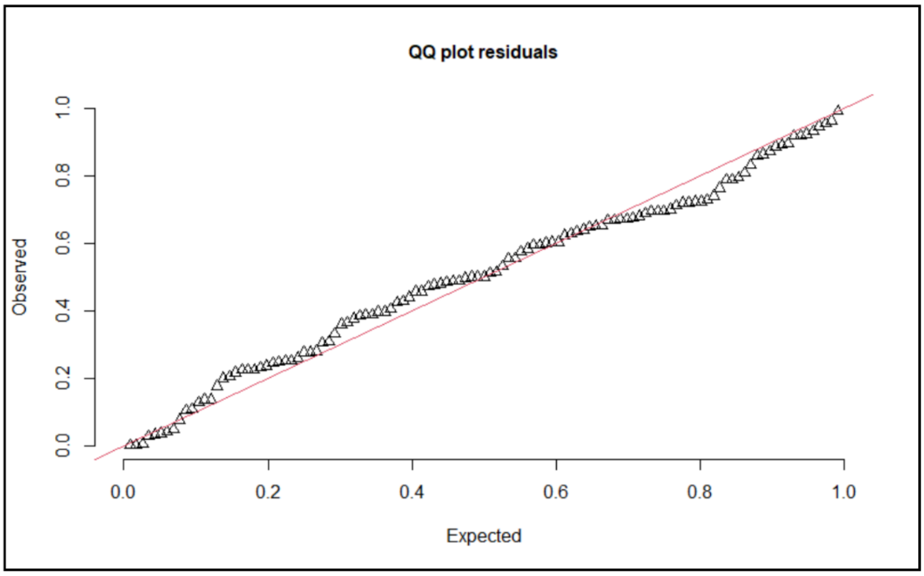

Figure A.2: QQ-plot of GLMM using the Gower Similarity Index as response and time since restoration as predictor.

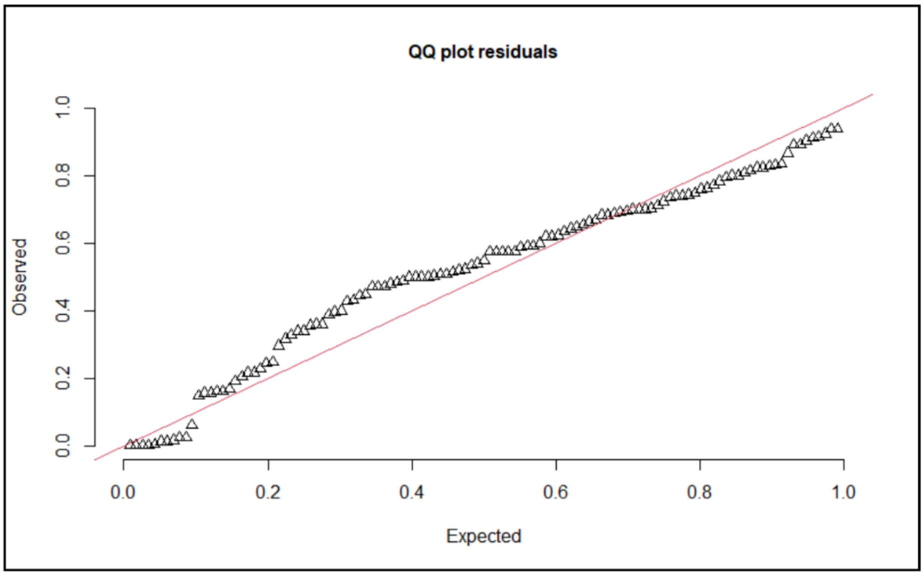

Figure A.3: QQ-plot of GLMM using the Saprobic Index as response and Time since restoration as predictor.

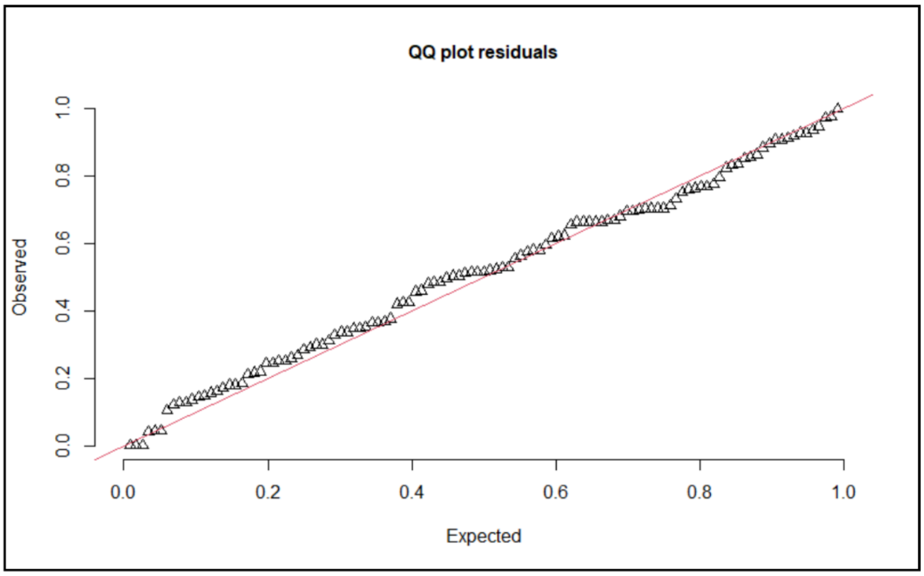

Figure A.4: QQ-plot of GLMM using the Chloride Index as response and Time since restoration as predictor.

## Appendix B: Test for spatial autocorrelation

We used the testSpatialAutocorrelation function from the package “Dharma” which uses Moran’s I test to determine if there is spatial autocorrelation in our models that included a spatial autocorrelation structure.

1.) Saprobic Index

Example of R code used to test for spatial autocorrelation:

```
simres   <- simulateResiduals(model)

groupsim <- recalculateResiduals(simres,  group=Sap_Boye$a)

testSpatialAutocorrelation(groupsim,x=unique(Sap_Boye$X_UTM32),
y=unique(Sap_Boye$Y_UTM32))
```

R output:

```
DHARMa Moran's I test for distance-based autocorrelation

data:  groupsim

observed = -0.019741, expected = -0.100000, sd = 0.096621, p-value = 0.4062
```

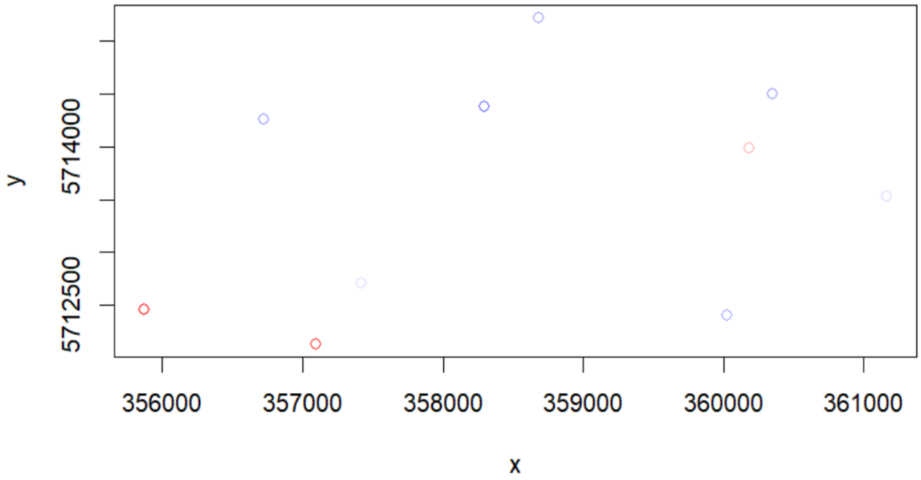

Figure B.1: DHARMa Moran’s I test for distance-based autocorrelation for the model of the Saprobic Index.

2.) Chloride Index

R output:

```
DHARMa Moran's I test for distance-based autocorrelation

data:  groupsim

observed = -0.066354, expected = -0.100000, sd = 0.104861, p-value = 0.7483
```

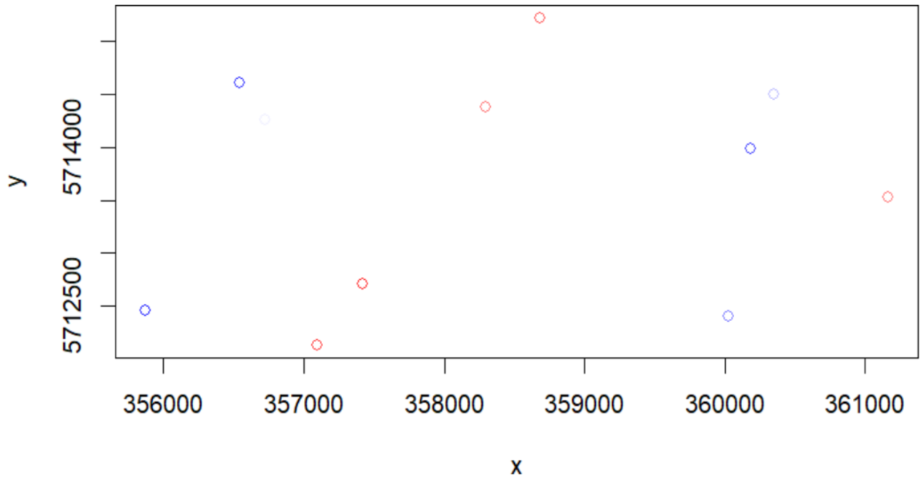

Figure B.2: DHARMa Moran’s I test for distance-based autocorrelation for the model of the Chloride Index.

3.) Dispersal Index

R output:

```
DHARMa Moran's I test for distance-based autocorrelation

data:  groupsim

observed = -0.054372, expected = -0.100000, sd = 0.101277, p-value = 0.6523
```

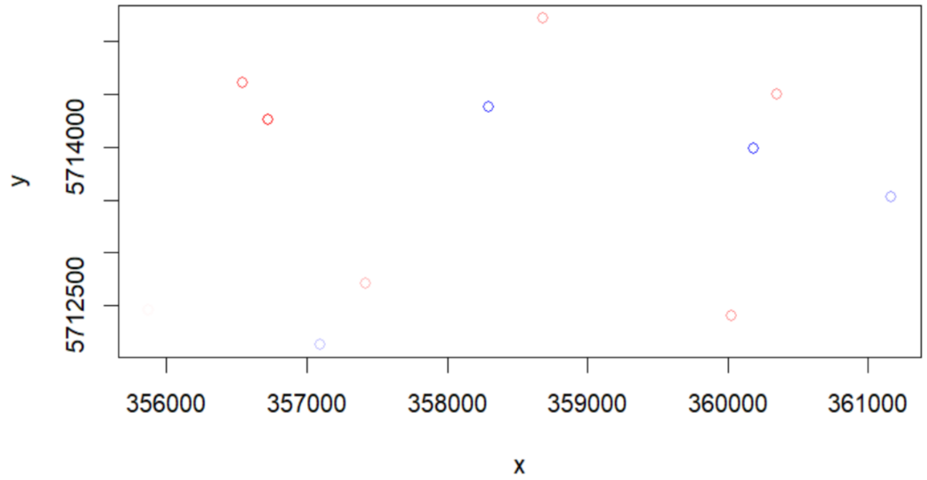

Figure B.3: DHARMa Moran’s I test for distance-based autocorrelation for the model of the Dispersal Index.

4.) Gower Similarity Index

R output:

```
DHARMa Moran's I test for distance-based autocorrelation

data:  groupsim

observed = -0.037726, expected = -0.100000, sd = 0.099451, p-value = 0.5312
```

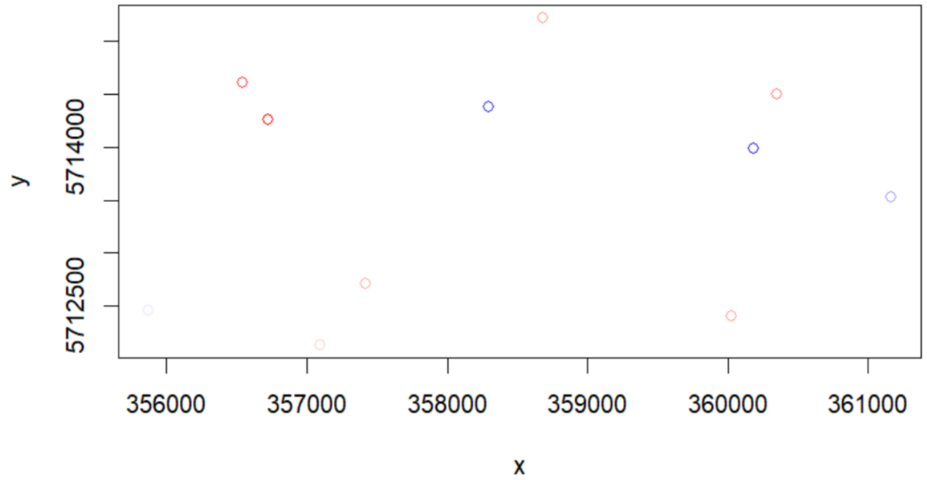

Figure B.4: DHARMa Moran’s I test for distance-based autocorrelation for the model of the Gower Similarity Index.

None of the tests were significant. Therefore, including a spatial autocorrelation structure in our final model is unnecessary. Including it anyway leads to overfitting of the model. In the following, we explain this issue in more detail, based on an example.

### Example of a not-overfitted vs. an overfitted model

In the beta-model where phi is the scale parameter this parameter models variability/dispersion of the data.

Under normal conditions the smaller phi, the more variability in the data. It is often somewhere ~<1000 for a **not-overfitted model**.

Example data can be simulated using the estimation from the model given in the manuscript. Hereby we use phi = 300.

R-code for a not-overfitted model:

```
library(glmmTMB)
set.seed(123)
par(mfrow=c(1,2))

phi <- 300
x <- sample(-1:20, 70, replace=T)
y <- plogis(-0.01*x+0.33)
d <- rbeta(length(y), y*phi, (1-y)*phi)
plot(x, d, xlab="time", ylab="response", main="not-overfitted')
```

### For an overfitted model

When using the model “betamod_sap” with correction for autocorrelation, phi was 18931423. The R-squared was 0.99 which means the model fits all data points. This is illustrated in Figure B.5. This overfit is not the result of the fixed component (-0.01) but due to the model trying to account for the non-existing residual spatial-autocorrelation, eventually overfitting the model.

R-code for an overfitted model:

```
phi <- 18931423

x <- sample(-1:20, 70, replace=T)

y <- plogis(-0.01*x+0.33)

d <- rbeta(length(y), y*phi, (1-y)*phi)

plot(x, d, xlab="time", ylab=NA, main="overfitted')
```

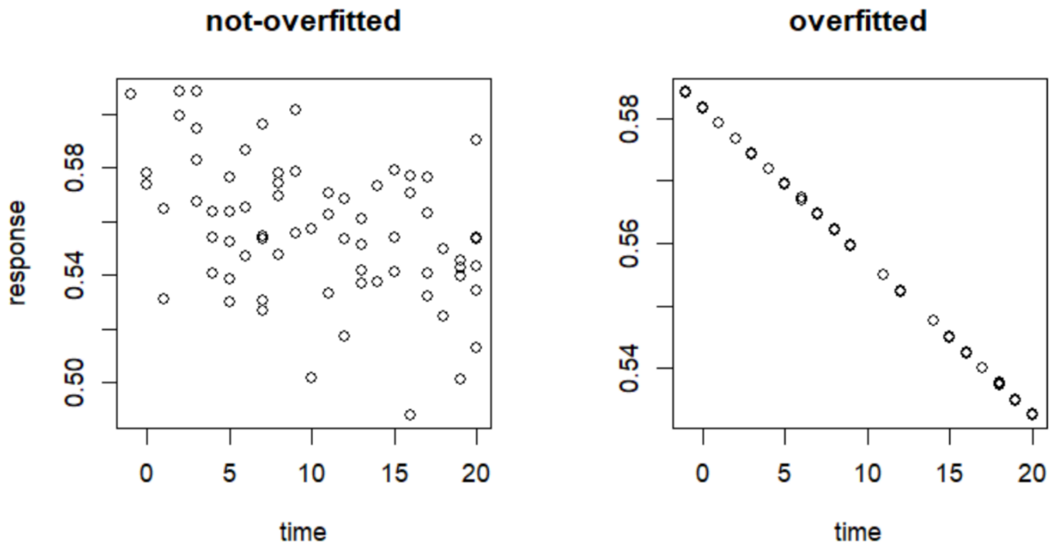

Figure B.5: Plots of the residual structure of a not-overfitted vs. an overfitted model.

## Extent of Contribution

Cumulative thesis of Svenja M. Gillmann

### Author contributions

Title: *How tolerances, competition and dispersal shape benthic invertebrate colonisation in restored urban streams*

Authors: Gillmann, S.M., Lorenz, A.W, Kaijser, W., Nguyen, H.H., Haase, P. and Hering, D.

Contributions:

- Conception - 90%
- Conduction of experimental work - 25%: field sampling
- Data analysis - 70%
- Species identification - 35%
- Statistical analysis - 80%
- Writing the manuscript - 90%
- Revision of the manuscript - 80%

Unterschrift Doktorand/in

Unterschrift Betreuer/in

# Chapter 3

## Contributions of source populations, habitat suitability and trait overlap to benthic invertebrate community assembly in restored urban streams.

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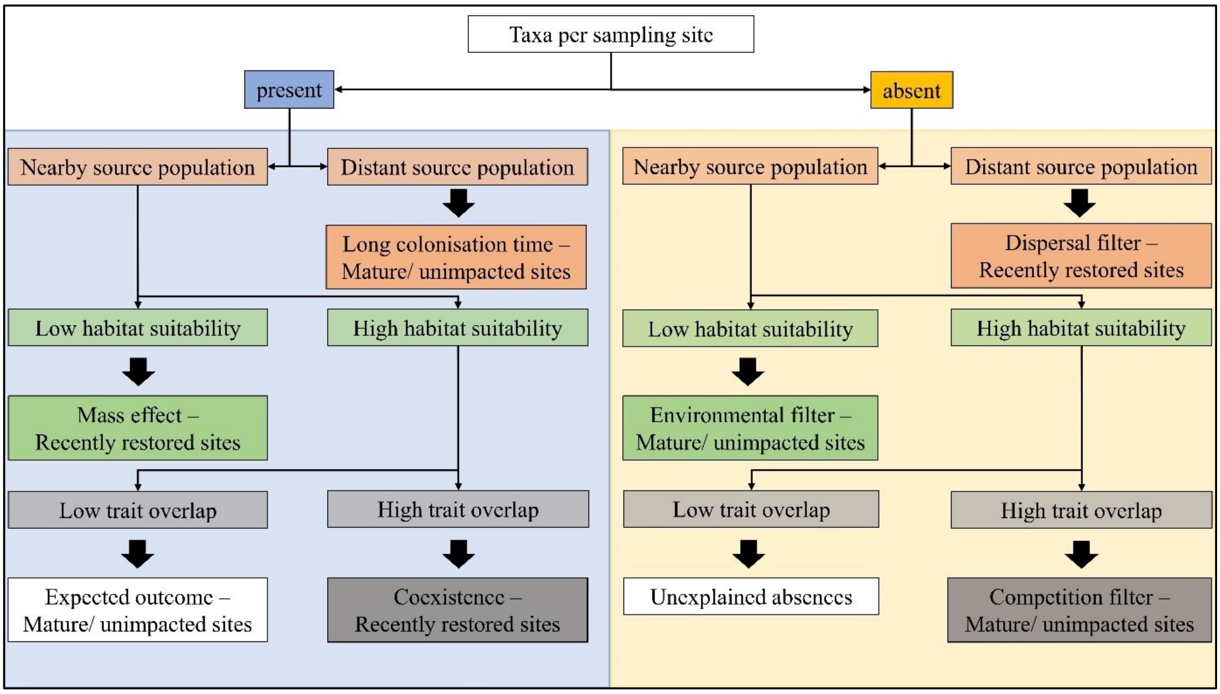

# Contributions of source populations, habitat suitability and trait overlap to benthic invertebrate community assembly in restored urban streams

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## Abstract

Community development in restored streams is often slow or even absent, but reasons remain obscure. Inadequate restoration measures, catchment-scale pressures, community closure and colonization barriers all may prevent or slow down recovery processes. For initial colonization, dispersal processes are supposed to be most important, which are referred to as dispersal filter. Environmental conditions of a restored reach determine if a dispersing species can successfully establish (environmental filter). Lastly, while available niches at those reaches fill up, biotic interactions, such as competition, become more important (biotic filter). To investigate the importance of these different filters, we compared benthic invertebrate communities of 20 sites in the Boye catchment (Western Germany), a former open sewer system. The sites were grouped, based on the years since restoration, into ‘unimpacted’ (never restored), ‘recently restored’ (< 4 years) and ‘mature restored’ (> 10 years) sites. Data collected at 28 additional sites in the catchment informed us on distances to potential source populations. Habitat suitability describes the fit between environmental conditions (abiotic site data) and species preferences and was used to assess the role of environmental filtering. We evaluated the role of the biotic filter based on trait overlap, referring to possible interspecific competition.

Communities collected at recently restored sites differed from those of mature restored and unimpacted sites. Taxa present at recently restored and mature sites had closer source populations than those of unimpacted sites. Taxa at mature and unimpacted sites had a better fit to the present habitats than those of recently restored sites. The trait overlap did not differ between co-occurring and not co-occurring taxa at any of the site groups. Our findings show that communities of mature restored sites that have been restored more than 10 years ago, resembled those of unimpacted sites. Dispersal was most important in early years of recovery. Taxa occurrences at sites with nearby source populations and low habitat suitability are likely the result of high rates of dispersal from upstream sources (mass effects). These can be caused by hatching events or environmental disturbances. Habitat suitability played a larger role for communities at mature and unimpacted sites which indicates that optimal communities shape over time. We did not find indications that competition played a role for community assembly. Hence, dispersal and habitat suitability were most relevant for species’ occurrences. Competition could be more important on micro scales and the results may differ if species abundances are taken into account.

## Introduction

The recovery of aquatic communities after pressure release can take multiple pathways (Sarr, 2002; Vos et al., 2023). These range from persistence of the degraded community (Lorenz et al., 2018) to full recovery (Clements et al., 2021). The degree of recovery depends on successful colonisation of a diverse community. However, even if communities recover at first, new and/or persisting pressures can interrupt and stop the progress of recolonisation (Haase et al., 2023). Understanding the processes that govern community assembly, is crucial to improve planning of future restoration measures and efficiently support stream communities on their way to full recovery.

From a more theoretical viewpoint, recovery processes are closely related to metacommunity theory. Metacommunity assembly is governed by spatial and local processes (Leibold et al., 2004; Lake et al., 2007; Vos et al., 2023). The dispersal ability of a species, the distance to source populations and dispersal barriers represent the first filter that determines whether a restored reach will be colonised (Lake et al., 2007; Sundermann et al., 2011; Tonkin et al., 2014). Consequently, good dispersers are the first to reach those sections (Winking et al., 2016; Baumgartner & Robinson, 2017; Lorenz et al., 2018), which is expected to be most relevant in the starting phase of community recovery (Vos et al., 2023). However, dispersal capacity loses importance with increasing connectivity (Brederveld et al., 2011). Recolonisation is particularly strong when source populations are in close proximity to the recovering stream reach and mass effects occur ( Leibold et al., 2004; Heino et al., 2015; Brown et al., 2018; Tonkin et al., 2018). These describe the phenomenon that species occur in unsuitable habitats, due to high rates of recurring dispersal from nearby source populations (Leibold et al., 2004).

The environmental filter, or suitability of a given habitat, eventually determines whether the colonising species can establish a population (Lake et al., 2007). Streams provide a variety of habitats and thus ecological niches which are colonised by aquatic biota according to their preferences (Schmera et al., 2017). The ecological niche is defined by the range of conditions relating to water quality, preferred habitat and food source (Soberon & Peterson, 2005). The niche theory distinguishes between the fundamental niche, which defines the conditions that are generally suitable for a given species and the realised niche, where the species actually lives under the conditions of competition and other biotic interactions (Soberon & Peterson, 2005). Aquatic communities therefore react sensitively to changes in the environmental conditions and stressed systems are only inhabited by tolerant species (Rumschlag et al., 2023). Thus, species tolerances against stressors are expected to be less important if restoration measures have reduced stress intensities (Vos et al., 2023). Within established communities, local dynamics are governed by biotic interactions, e.g. competition, which importance increases over time (Lake et al., 2007; Vos et al., 2023). Regional community dynamics are shaped by an equilibrium between local extinctions and colonisations, which can be driven by random processes (neutral theory) ( Leibold et al., 2004; Larsen et al., 2018) or short-term disturbances.

These processes acting during community assembly are closely intervened, thus, it is important to analyse their role for recolonisation simultaneously. However, while the processes have been analysed individually or in pairs, studies encompassing all three filters are lacking (Liu et al., 2023). Most studies focus on the influence of environmental and dispersal filters, while the role of biotic interactions is often neglected (Heino et al., 2015; Tolonen et al., 2018; He et al., 2023; Zheng & Yin, 2023).

Among riverine organisms, benthic invertebrates are an ideal group to test metacommunity theory. They are species-rich, their ecological preferences are well understood, and they contribute to a range of functional processes of streams, e.g., decomposition of organic matter (Palmer & Poff, 1997; Schmera et al., 2017). Benthic invertebrate species differ in sensitivity toward environmental changes, dispersal capacity and ecological niches (Jowett & Richardson, 1990; Kenney et al., 2009). Their specific preferences for environmental conditions can be used in habitat suitability models, to predict their potential occurrence in stream networks (Hirzel & Le Lay, 2008) and analyse changes in community composition (Lee et al., 2023), Recently, species preferences were fed into the models as prior knowledge, to improve the performance of the models (Vermeiren et al., 2020, 2021). However, integrating dispersal and biotic interactions into habitat suitability models is difficult, and has rarely been done (Schuwirth et al., 2016).

For a detailed assessment of the three community assembly filters (dispersal, environment, biotic interactions), extensive monitoring of the recovering communities is needed. Previous studies revealed that a benthic invertebrate community needs at least eight years to reach a certain maturity after restoration ( Lorenz, 2020; Gillmann et al., 2023) . Depending on the size of the restoration measures, new habitats have to develop first, before a stable community can establish (Pilotto et al., 2022). Further, restored sites were shown to be more rapidly colonised, if source populations are within close proximity (Sundermann et al., 2011; Tonkin et al., 2014). Vos et al. (2023) predicts the role of dispersal, tolerance and competition to change over time, with dispersal being most important in the first phase of recolonisation, before environmental filters and biotic interactions gain relevance. These predictions were generally supported by Gillmann et al. (2024): The analysis of 10-year post-restoration benthic invertebrate community assembly revealed that dispersal capacity and tolerance toward organic decomposition decreased with time since restoration, while interspecific competition increased. While this previous study revealed how the three filters generally change over time at the community level, it does not provide a species- and site-specific analysis. The environmental filter was only analysed in terms of tolerance toward chloride and organic decomposition, without considering substrate availability and other abiotic factors. Additionally, mean community dispersal capacity only gives limited information on the presence of a dispersal filter.

Here, we used data of benthic invertebrate communities, collected at specified distances, to gain information on potential source populations for our 'main sites'. To investigate the role of the environmental filter, we matched the abiotic site data ('site profiles') with the species' preferences ('species profiles'), which resulted in a measure of habitat suitability (Vermeiren et al., 2020). Trait overlap served as a proxy for biotic interactions. With this detailed dataset we compared how the role of the three filters differs between sites of different maturity stages. More specifically, we hypothesized that (1) the community composition of recently restored sites differs from those of mature and unimpacted sites, as new habitats are still developing and not all potential taxa reached the restored sites. (2) The closer the nearest source population, the more likely is a species' occurrence. This is particularly relevant for recently restored sites, and less for mature and unimpacted sites. (3) The better the 'species profile' matches the 'site profile', the more likely is its occurrence. This 'environmental filtering' is supposed to be less relevant for the recently restored sites, but most relevant for mature and unimpacted sites. (4) The more strongly traits of a given species overlap with species established at a site, the less likely is its occurrence. This biotic filtering is particularly relevant for mature and unimpacted sites.

This study aims at a deeper understanding of metacommunity assembly, by capturing the major assumptions of the Asymmetric Response Concept (ARC; Vos et al., 2023) in detail. The comparison of different maturation stages of restored sites will help to inform managers, which actions are most important during the respective phases of recovery.

## Methods

### Sampling

The Boye is a tributary to the Emscher catchment, located in Western Germany. The Boye and most of its tributaries were used as open sewers for several decades. At the end of the 20th century, the sewage system was moved underground and the impacted streams were gradually released from wastewater, followed by hydromorphological restoration. Restoration measures at the last stream reaches were finalised in 2021. A more detailed description of these measures and the Boye catchment itself is provided in Gillmann et al. (2023).

In total, 48 sites were sampled for their benthic invertebrate community. Twenty of the sites are part of an annual monitoring program, established for the RESIST project ('main' sites in Fig. 1). These were grouped according to the time of their completed restoration into 'unimpacted' (never carried wastewater), 'mature restored' (restored > 10 years prior sampling) and 'recently restored' (restored < 4 years prior sampling). To gain information on potential source populations for these sites, additional 28 sites ('source' sites in Fig. 1) were distributed in the catchment and sampled in 2022. These sites were placed 1 km and 2 km upstream of each main restored site. If possible, an additional site was located in the upstream sections of the streams that never carried wastewater. The unimpacted 'main' sites were considered as potential 'source' sites; hence, no additional sites were sampled upstream of these if they were within the 2 km distance of another main site.

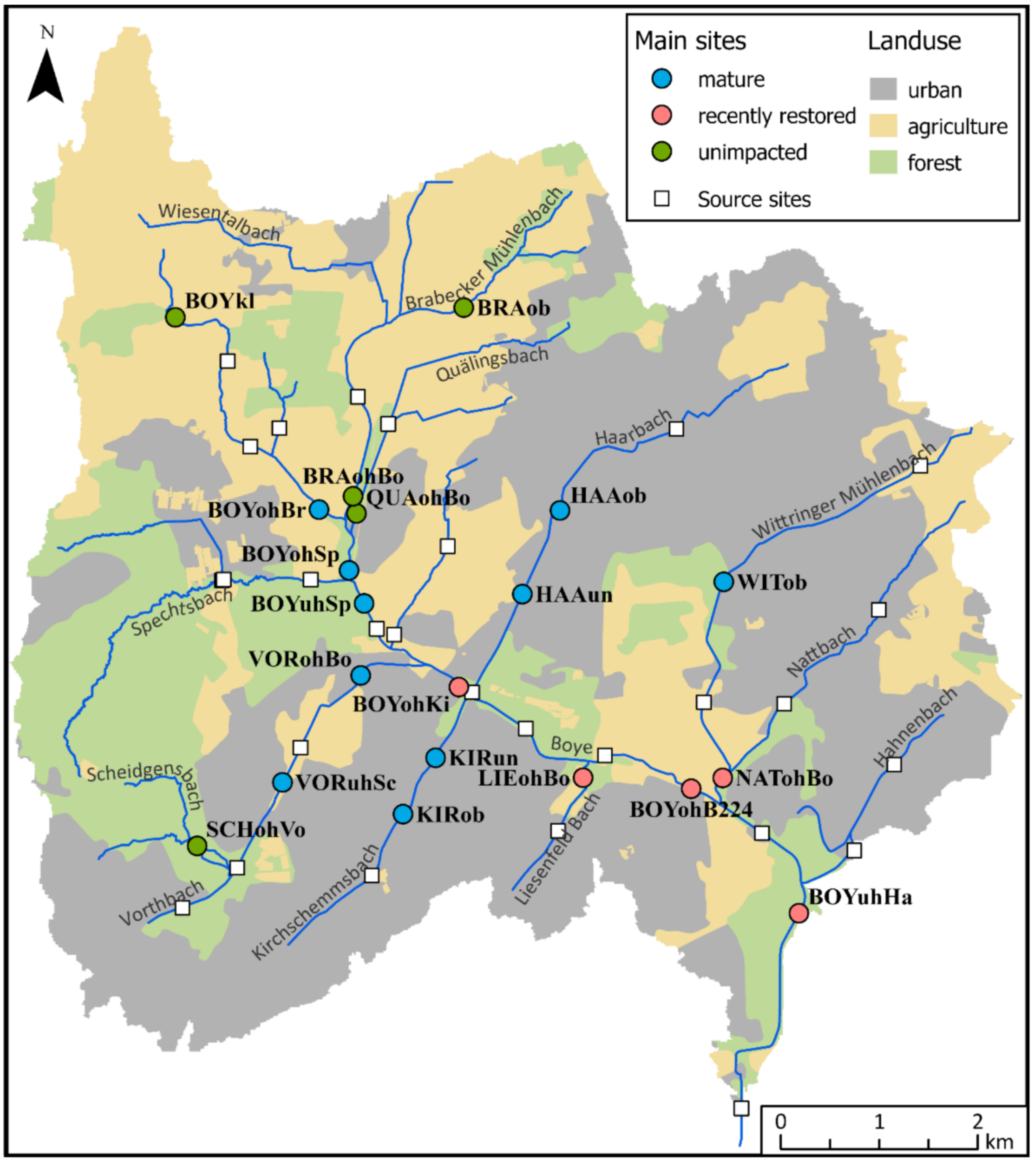

Figure 1: Map of the Boye catchment (Ruhr Metropolitan Area, Western Germany). The 'main' sites are displayed with dots, colored according to their site group: mature (blue), recently restored (red), unimpacted (green). The 'source' sites, located 1 and 2 km upstream of each main site, are displayed as white boxes. Three major types of land use of the catchment (merged from CORINE and InVeKos) are displayed in different colors: urban (grey), agriculture (yellow), forest (green).

All benthic invertebrate samples were collected following the standardised protocol for multi-habitat sampling (Haase et al., 2004). The collected samples were preserved in ethanol (96%) and brought back to the laboratory for further processing. The 'main' sites are part of an annual sampling campaign. To comply with the methods used in previous years, these samples were sorted and identified morphologically, according to the operational taxalist for Germany (Haase et al., 2006), resulting in a list with species abundances.

Standard methods for monitoring of benthic invertebrates (Haase et al., 2006) provide reliable information about abundances but are time consuming. Alternative methods based on eDNA and DNA metabarcoding techniques (Elbrecht et al., 2017) allow high throughput but provide only presence/absence information. Hence, we used DNA metabarcoding to identify the samples of the 'source sites' (Buchner et al., 2021) and adjusted them to the same taxonomic level as the 'main' sites.

### Environmental data

At all sites, the proportions of available stream bottom substrate were recorded in 5% increments, as specified in the standardized protocol for MHS (Haase et al., 2004). Single measurements of oxygen, temperature, conductivity, and pH were recorded for the 'main'- and 'source' sites. More detailed physico-chemical parameters were collected only at the 'main' sites: Upon MHS, flow velocity was measured at each location of sample unit collection and summarised into a mean flow velocity per site. Additionally, two loggers per site recorded water temperatures at 30-minute intervals. We used the data collected from June until September 2021, i.e., the year before sampling of benthic invertebrates, to determine mean summer water temperatures. Lastly, water samples were collected bi-weekly, starting in March 2021, which were stored at -20 °C before analysis commenced in the laboratory. Concentrations of ammonium, nitrate, dissolved oxygen content (DOC) and orthophosphate were derived from the water samples. In combination with the oxygen content, measured on site, they were used to determine the water quality classes related to saprobity.

### Data preparation

### Distance to source populations

We calculated the terrestrial and instream distance between the 48 sampling sites. Only distances to the upstream sites were considered for further analysis. Taxa were grouped into holo- and merolimnic taxa. For every combination of taxon and site, we determined the terrestrial and instream distance to the closest source population, meaning the next upstream site with an occurrence of the taxon. For hololimnic taxa, only the instream distance was considered, while for merolimnic taxa, the smaller of the instream and terrestrial distances was considered as closest distance to the next source population.

### Environmental filtering

We analysed the role of environmental filtering for the 20 ‘main’ sites by calculating habitat suitability values per species and site. To this end, we compared ‘species preference profiles’ with the environmental conditions at each of the ‘main’ sites: substrate proportions, mean flow velocity, mean summer temperature and saprobic classes. For the species preference profiles, the following parameters were collected: microhabitat preferences, saprobic values and indicator weights, KLIWA index and specificity value (freshwaterecology.info; Schmidt-Kloiber & Hering, 2015) and flow velocity preference (STOWA database; Verberk et al., 2012).

Habitat suitability was derived for the parameters, ‘substrate’, ‘saproby’ and ‘temperature’ for each combination of site and species. To compare the present substrates with the taxa preferences, some of the substrate categories were combined to fit the categories of substrate preferences as defined in freshwaterecology.info (Appendix S1, Table S1). The taxas’ saprobic values and indicator weights were compared to the saprobic classes of each of the sampling sites as derived from water quality parameters. Saprobic classes were calculated based on the class borders defined by the LAWA, in 1998, published by Bernatowicz et al. (2009)see also Appendix S1, Table S2). For the calculations, the data collected from the bi-weekly water samples in 2021 was used. The following parameters were included in the calculation: minimum oxygen contents, maximum ammonium, maximum nitrate, total ammonium and median nitrate, mean DOC, maximum and median orthophosphate. For water temperature, we used the logged temperatures from summer 2021 (June until September), as the corresponding biotic metric (the KLIWA index) is based on the summer mean and maximum temperatures.

The habitat suitability functions quantify how the habitat’s suitability for each taxon varies with each environmental variable, scaling from zero to one. They consist of preference scores, which are normalized to values between zero and one, and a linear interpolation to derive a continuous function from discrete classes of the environmental variable (see Appendix S1, Table S3). This approach has previously been used by Vermeiren et al. (2020), where the habitat suitability served as prior knowledge input in habitat suitability models. Instead of using a full habitat suitability model, which would require a larger number of sites for calibration, we used the habitat suitability functions directly to predict species occurrences and absences. To this end, we calculated the mean habitat suitability from all environmental factors.

### Biotic interactions

The resource use of benthic invertebrates is mainly defined by its feeding type and microhabitat preference. Therefore, we utilized these two key traits to analyse biotic interactions between taxa in terms of trait overlap. After downloading the trait information from freshwaterecology.info (Schmidt-Kloiber & Hering, 2015), we quantified the trait overlap using the 'gawdis' function (Bello et al., 2021), resulting in a Gower Similarity index, spanning between 0 and 1, for each species pair. We defined the highest possible match between traits of different taxa as the degree of possible competition between them. Therefore, we determined the maximum trait overlap per taxon for co-occurring or not co-occurring taxa.

### Data analysis

We calculated the Jaccard dissimilarity between communities, based on the presence/ absence taxalist of the 'main sites', using the function 'vegdist' (package 'vegan', v.2.6-4, Oksanen et al., 2024). With the function 'metaMDS' (package 'vegan', v.2.6-4, Oksanen et al., 2024), we visualised the community distances using Non-metric multidimensional scaling (NMDS, k=3). The site labels include the stream, where the site is situated (first three letters), and the description of the location within the stream (fourth letter onward). The difference between the different site groups ('unimpacted', 'recently restored', 'mature restored') was tested, using the Analysis of Similarities (ANOSIM) statistics (function 'anosim', package 'vegan', v.2.6-4, Oksanen et al., 2024).

We separately analysed each of the three factors (dispersal, environmental filtering and biotic interactions) and compared values between the present and absent communities. To visualize changes in the proportions of present and absent taxa along the gradients of the different filters, we summarised the number of cases for subgroups along these gradients. The distance to the nearest source was used to quantify the dispersal filter. Due to our sampling design, most sites were 1 km apart, however, some 'main' sites were closer together. To consider these smaller scales, we divided the groups in 500 m steps, resulting in 18 groups. Cases, where taxa had no upstream source population were grouped together as 'no source' (19th group). The mean habitat suitability and maximum trait overlap, both ranging from zero to one, were divided into 10 groups. For each group per factor, we calculated the proportions of present vs. absent taxa. In addition, we determined the total number of cases, contributing to each proportion per subgroup.

We used logistic regression models to analyse the probability of species occurrence per factor for all sites. Therefore, we constructed binomial generalised linear mixed models (GLMMs) with ‘logit’ link function (package ‘glmmTMB’, v.1.1.8, Brooks et al., 2017), with occurrence as binary response variable. We used the factors (distance to nearest source population, mean habitat suitability, trait overlap) as fixed effect, respectively, and included the species as random effects. The conditional R-squared results from correlating the fitted with the predicted values. We checked the residuals, using the ‘simulateResiduals’ from the ‘DHARMA’ package (v.0.4.6, Hartig & Lohse, 2022).

For each factor, we analysed the difference between groups of occurrence and groups of sampling sites (i.e., ‘unimpacted’, ‘recently restored’ and ‘mature restored’ sites). The spread of the data was visualised using boxplots. To statistically determine the difference between groups, we constructed different models per factor. For the distance to the nearest source, we used a GLMM with gamma distribution (package ‘glmmTMB’, v.1.1.8, Brooks et al., 2017). For habitat suitability and trait overlap, we used generalized additive models with beta and beta one inflated distributions (package ‘gamlss’, v. 5.4, Rigby & Stasinopoulos, 2005). All models treated ‘occurrence’ and ‘site group’ as fixed effects and ‘species’ as random effect. We extracted the estimated marginal means (EMMs) from the models using the function ‘emmeans’. From the same package, we used the function ‘pairs’ to determine the significance of differences between present and absent taxa per group, which conducts a post-hoc test between the EMMs of different groups, while considering unequal number of observations and random effects (package ‘emmeans’, v. 1.10.2, Lenth, 2017).

All data was analysed in R (v.4.1.2, R core Team, 2021) and visualised with the package ‘ggplot2’ (v.3.4.1, Wickham, 2016).

## Results

### Description of the benthic invertebrate communities

In total, we identified 107 different taxa at the main sites in the Boye catchment. Individuals belonging to the family of Chironomidae occurred at all main sites. The taxa identified to species level with the highest prevalences were *Gammarus pulex*, *Limnephilus lunatus* and, *Prodiamesa olivacea*. They occurred at 18 of the 20 main sites. Our dataset included 34 taxa that each occurred at only one of the main sites. 37 taxa were only found at source sites.

## Differences between benthic invertebrate communities

The NMDS (Fig. 2, stress= 0.13) displays the Jaccard similarity between communities of the main sites. The communities of the mature and unimpacted sites are clustered close together, displaying their high degree of similarity. Three of the recently restored sites are clearly apart from the other communities, while one of the recently restored sites is more similar to the unimpacted and mature sites than to other sites of its group. The Analysis of Similarities (ANOSIM) confirmed a moderate difference between groups of sampling sites ($R^2$= 0.22, p= 0.02).

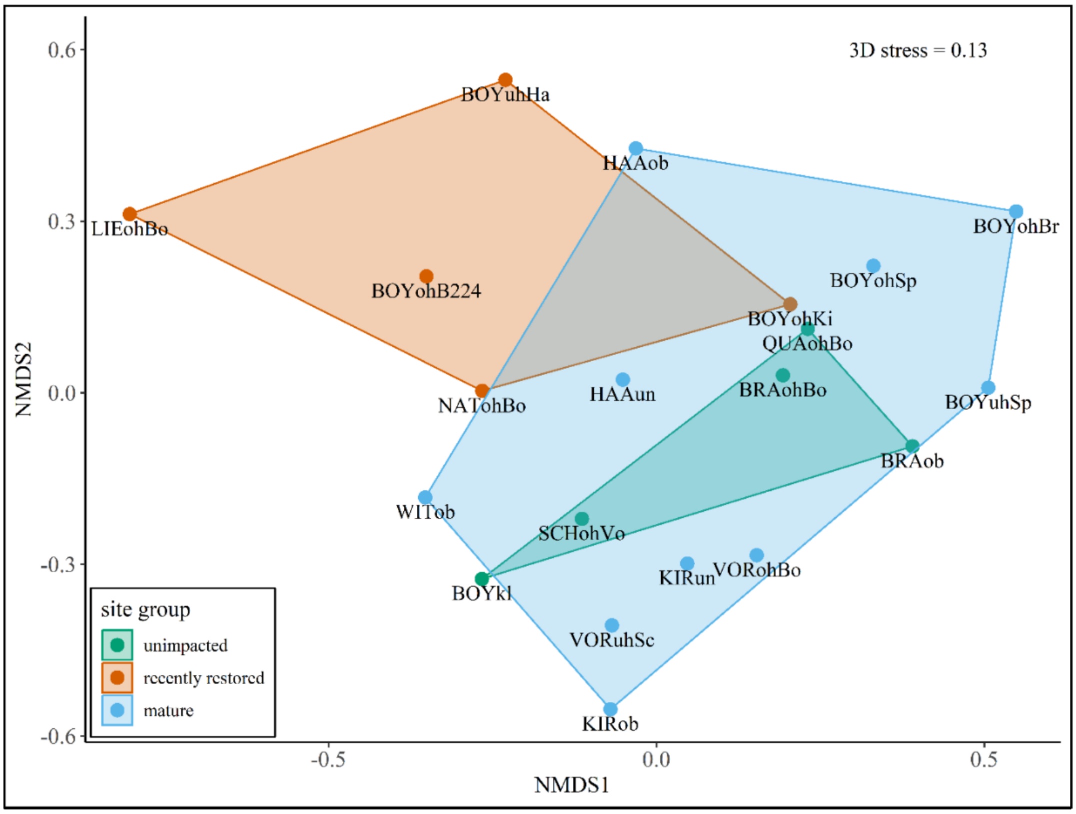

Figure 2. NMDS of Jaccard dissimilarities, derived from presence/ absence data of taxa found in the different sites (stress = 0.13). Differences between site groups were tested using the ANOSIM statistics ($R^2$= 0.22, p= 0.02).

## Dispersal filter

We determined the distance to the nearest source population for all taxa per site and analysed the changing proportions of present and absent taxa along the distance gradient. The proportion of present taxa decreases with the distance to the nearest source population (Fig. 3A). This pattern is supported by the underlying model which identifies a significant decrease in probability of taxa occurrence ($p < 0.05$, Fig. 3B) with increasing distance to the source. In the majority of cases, a source population is present within 1.5 km upstream. Only in one case, a taxon was found to occur with its nearest source population located at a distance > 5 km. In a large proportion of cases, absent taxa did not have an upstream source population within the Boye catchment which was true for fewer cases of present taxa.

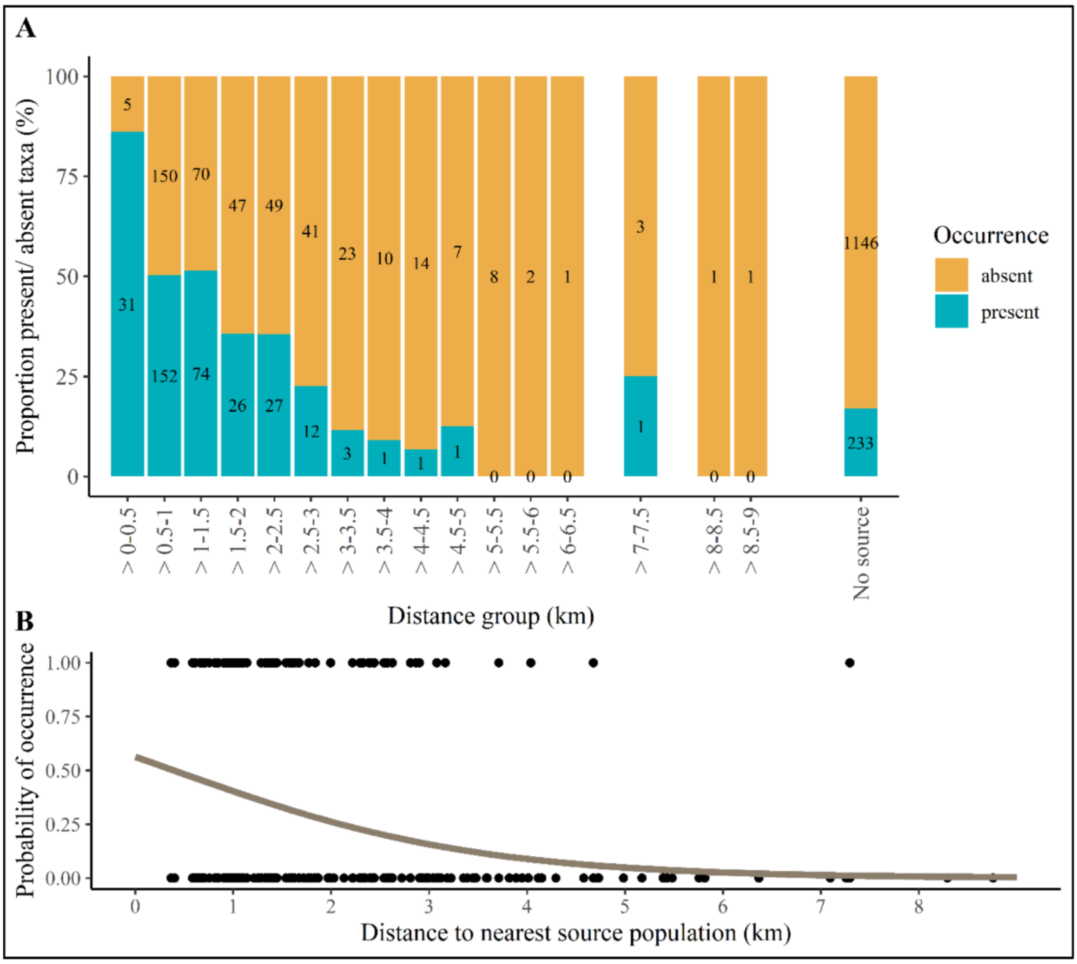

Figure 3. A: Proportion of present and absent taxa per distance group. The distances were discretized into classes of 500 m, resulting in 18 groups. Taxa that did not have an upstream source population were defined as 19th group. The number of 'absent' and 'present' cases is indicated in the corresponding bars. B: Logistic GLMM displaying the probability of occurrence in relation to distance to the nearest source population ($R^2 = 0.27$).

We determined the distribution of the distances to the nearest source population across unimpacted, recently restored and mature sites, categorized by 'absent' and 'present' taxa for each site group (Fig. 4). Statistical differences between groups were determined using estimated marginal means. At unimpacted sites, there is no significant difference in distance between 'absent' and 'present' taxa (p = 0.152). The distance to the nearest source population is significantly different between 'absent' and 'present' taxa for both, the recently restored and the mature restored sites ($p < 0.05$). In both cases, the distance to population sources is lower for the present taxa. However, the distribution of the data and estimated marginal means are larger for absent taxa at the recently restored sites compared to the mature sites.

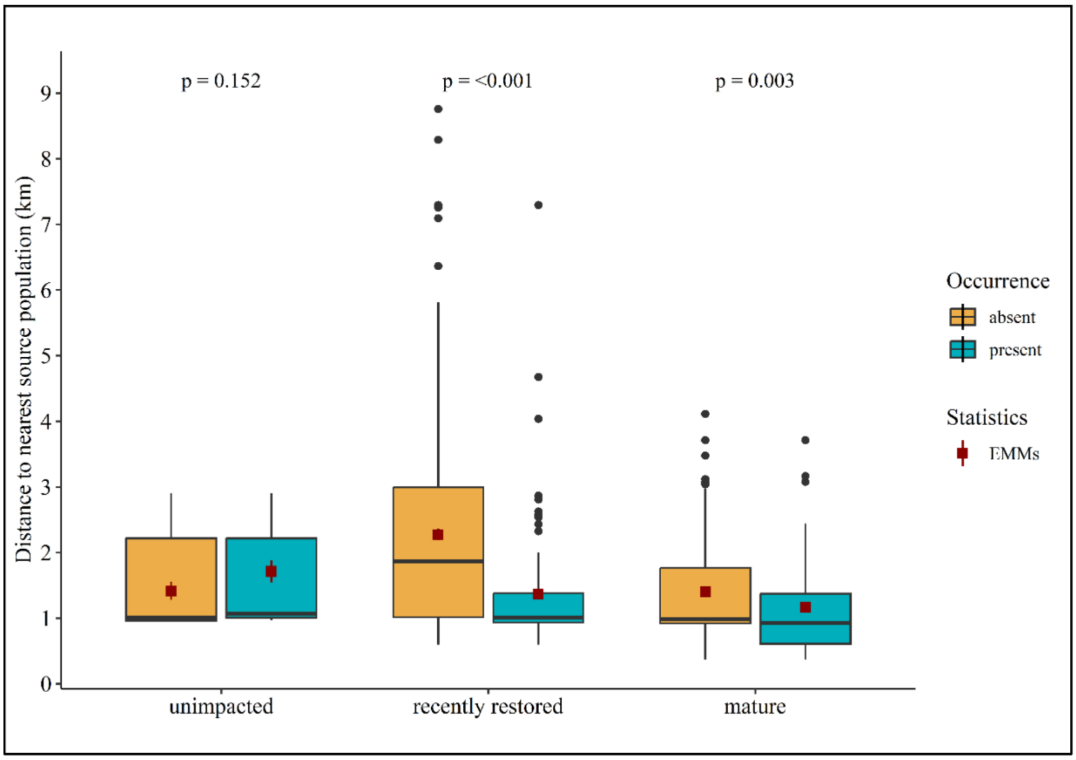

Figure 4. Boxplot of present and absent taxa and their distance to the nearest source population, grouped by maturation state. The difference between distances of the absent and present taxa were compared conducting a post-hoc test on estimated marginal means (EMMs). These were extracted from the corresponding generalised linear mixed model (GLMM), to account for different numbers of observations and to consider random effects. Estimated marginal means (EMMs) are represented by red boxes and corresponding error bars. Non-overlapping error bars indicate statistically significant differences ($p < 0.05$). For more detailed results on EMMs see Appendix S2, Figure S1.

Environmental filter

We used the mean habitat suitability to compare differences between present and absent taxa per site. The proportion of present species in all groups is below 50%, except for the group with the highest habitat suitability (Fig. 5A). The group with the lowest habitat suitability has the lowest proportion of present taxa. In the habitat suitability classes between 0.1 and 0.5 the proportion of present taxa varies around 25% and increases with increasing habitat suitability above 0.5. This increasing trend is mirrored in the modelled probability of taxa occurrence ($p < 0.05$, Fig. 5B). However, the two classes with the highest habitat suitability have the lowest number of cases (73 and 14). The largest number of cases belong to the group with mean habitat suitabilities between 0.6 and 0.7 (410 cases).

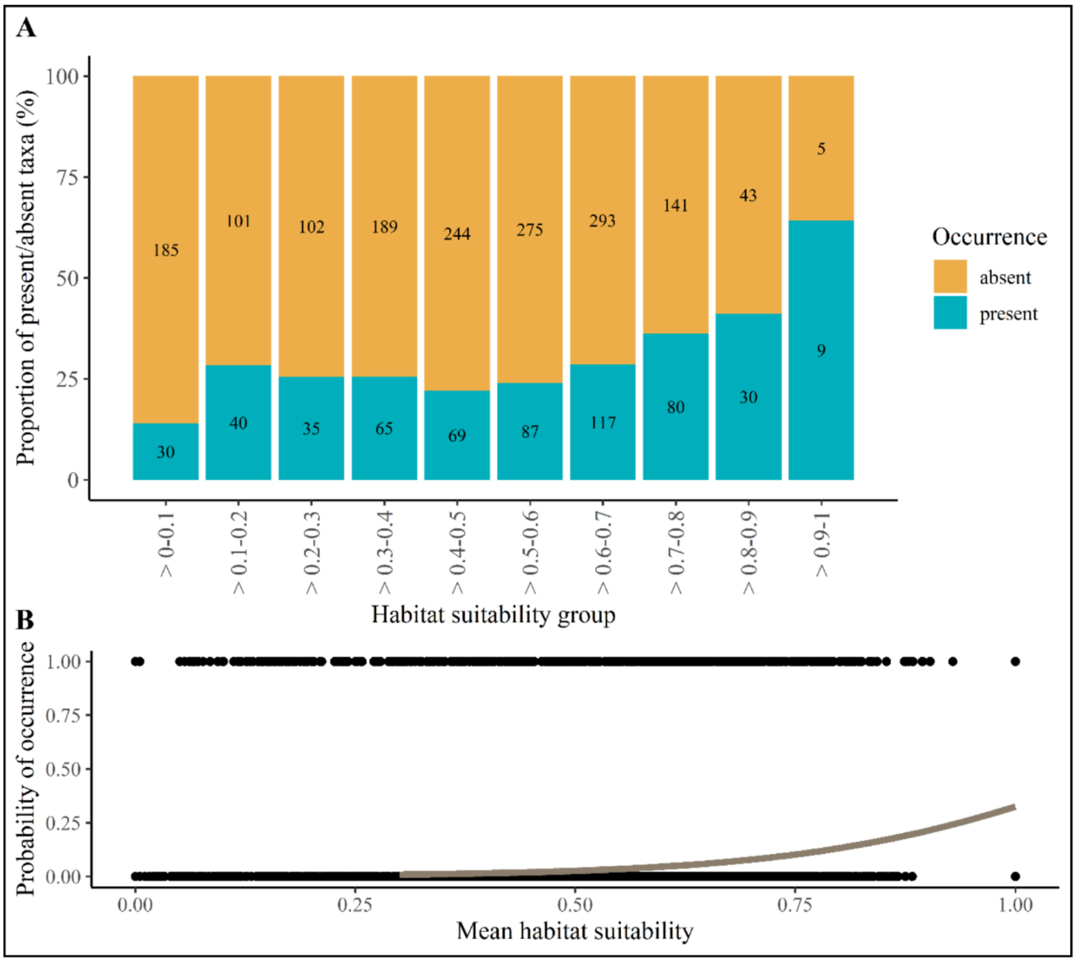

Figure 5. A: Proportion of present and absent taxa per habitat suitability group. The suitabilities were discretized into classes of 0.1, resulting in 10 groups. The number of 'absent' and 'present' cases is indicated in the corresponding bars. B: Logistic GLMM displaying the probability of occurrence in relation to mean habitat suitability ($R^2 = 0.01$).

Despite small differences in distributions, the mean habitat suitability is significantly higher for present taxa than absent taxa at unimpacted sites (Fig. 6, $p < 0.05$). A positive trend of the present taxa having higher suitabilities, as compared to absent taxa, is also observed at recently restored and mature sites. However, the difference at mature sites is only close to being statistically significant ($p = 0.068$), while at recently restored sites, it is not significant ($p = 0.357$).

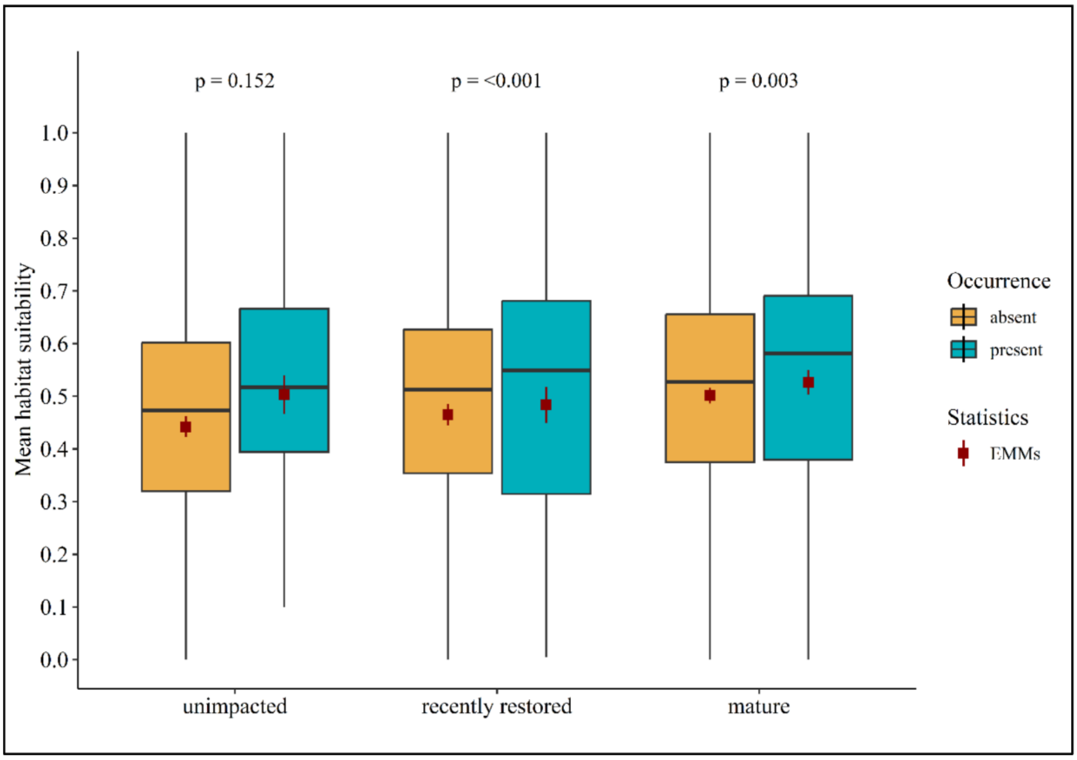

Figure 6. Boxplot of present and absent taxa and their mean habitat suitability. The difference between suitabilities of absent and present taxa were compared conducting a post-hoc test on estimated marginal means (EMMs). These were extracted from the corresponding generalised linear mixed model (GLMM), to account for different numbers of observations and to consider random effects. Estimated marginal means (EMMs) are represented by red boxes and corresponding error bars. Non- overlapping error bars indicate statistically significant differences ($p < 0.05$). For more detailed results on EMMs see Appendix S2, Figure S2.

Biotic interaction filter

We determined the maximum Gower Similarity, i.e., trait overlap, between taxa that were and were not co-occurring per site. The proportion of present taxa is lower than that of absent taxa in all groups (Fig. 7A). The highest number of cases have a maximum trait overlap between 0.7

and 0.9. Modelled probability of occurrence predicts an overall increase along the gradient. However, the regression coefficient was not significantly different from zero (p= 0.068, Fig. 7B).

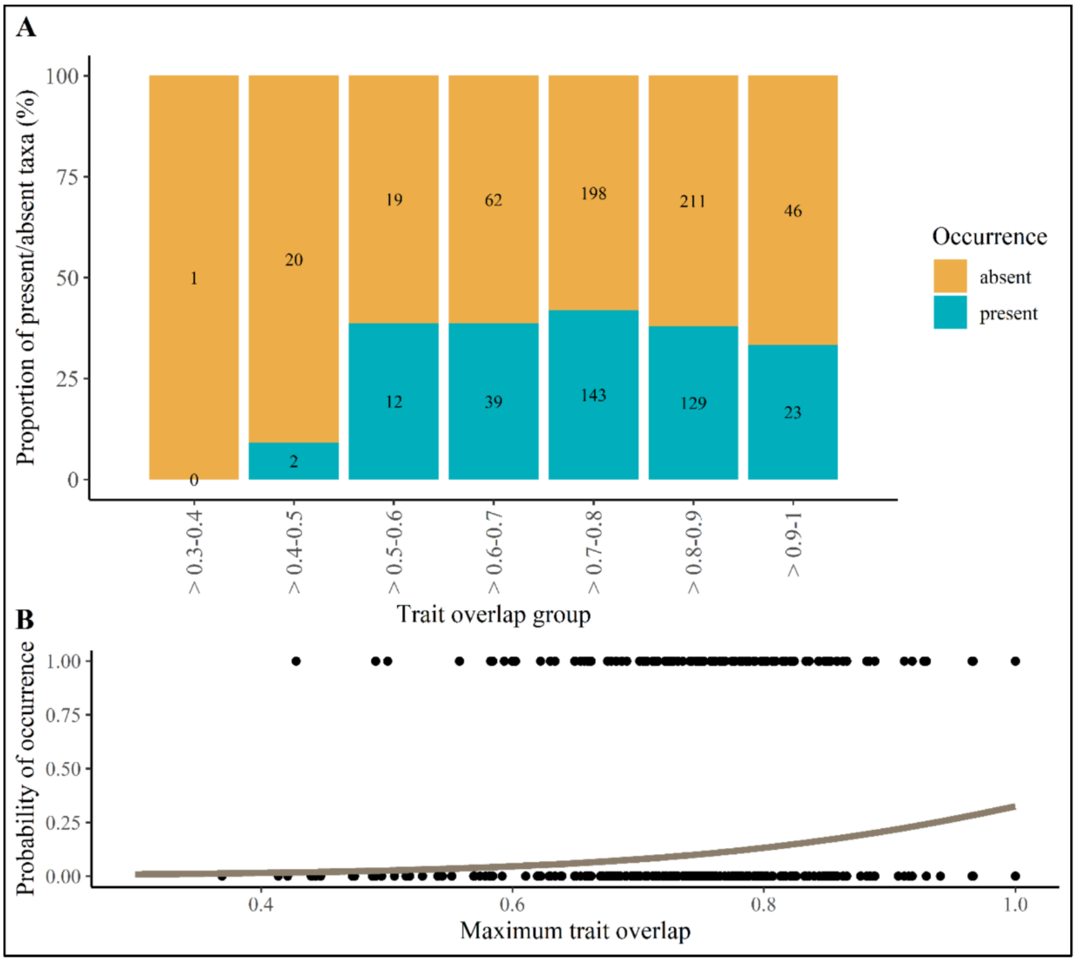

Figure 7. A: Proportion of present and absent taxa per trait overlap group. Trait overlaps were derived from the Gower similarities, calculated between co-occurring and not co-occurring taxa. Trait overlaps were discretized into classes of 0.1, resulting in 10 groups. The number of 'absent' and 'present' cases is indicated in the corresponding bars. B: Logistic GLMM displaying the probability of occurrence in relation to maximum trait suitability ($R^2 = 0.01$).

There are no significant differences in maximum trait overlap between co-occurring and not co-occurring taxa across the three groups of sites (Fig. 8). The median and EMM of the present taxa at unimpacted sites is slightly lower, however, this difference is not significant ($p > 0.05$). The spread of the data in the other groups is similar with no significant differences.

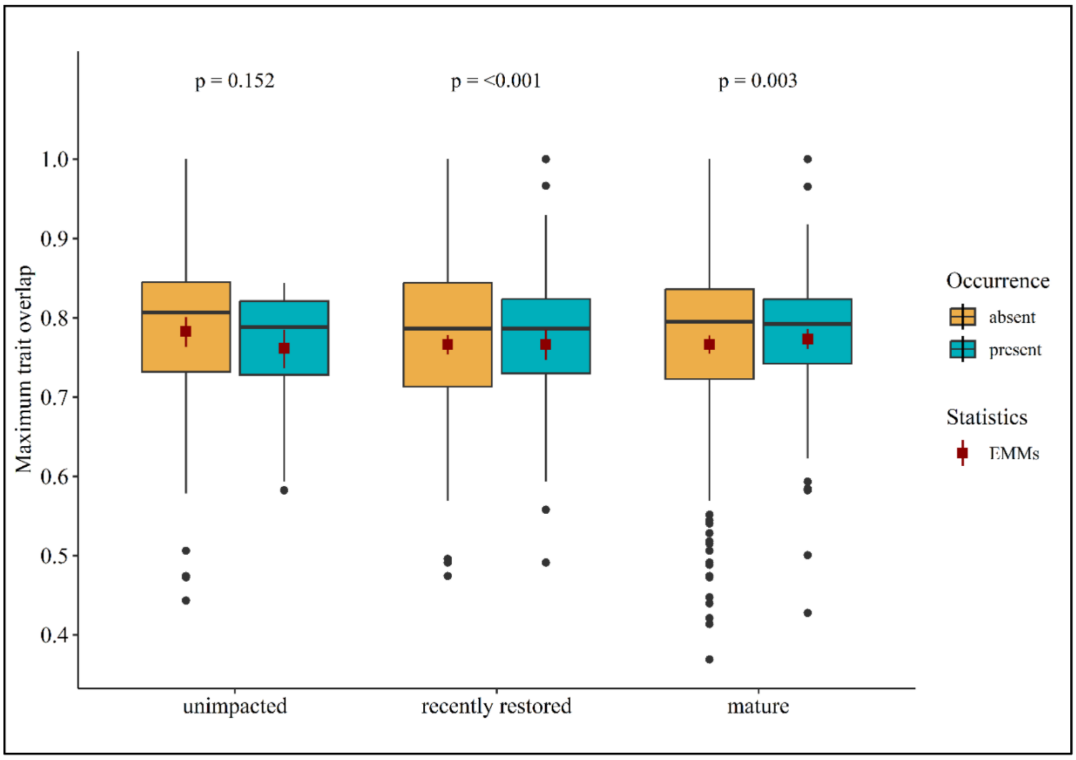

Figure 8. Boxplot of present and absent taxa and their maximum trait overlap. The difference between trait overlaps of absent and present taxa were compared conducting a post-hoc test on estimated marginal means (EMMs). These were extracted from the corresponding generalised linear mixed model (GLMM), to account for different numbers of observations and to consider random effects. Estimated marginal means (EMMs) are represented by red boxes and corresponding error bars. Non- overlapping error bars indicate statistically significant differences ($p < 0.05$). For more detailed results on EMMs see Appendix S2, Figure S3.

## Discussion

This study aimed to test the assumptions of the ARC with a recent and detailed dataset, comprising a total of 48 sites in the Boye catchment. More specifically, we challenged the assumption that the role of the colonisation filters, dispersal, environmental filtering and biotic interactions (competition) differs between stages of recovery. We first verified if the groups of sampling sites ('unimpacted', 'recently restored', 'mature restored') differ in their community composition, to justify further analysis. Indeed, the NMDS revealed that most communities of the recently restored sites (BOYohB224, LIEohBo, BOYuhHa, NATohBo) differ from those belonging to the other two groups. Additionally, the ANOSIM statistics suggested a moderate dissimilarity between groups which confirms our hypothesis (1) on differences between site groups. Similarly, Winking et al. (2014) found a significant difference between communities of recently restored sites (one to four years after restoration) and old restored sites (> 9 years after restoration) in the Boye catchment. The moderate outcome of the ANOSIM may be due to the generally low number of recently restored sites. Notably, the community at one of these sites (BOYohKi) was more similar to the mature Boye sites (BOY) than to the recently restored sites. However, this site is located in the middle of the catchment, in close proximity to the mouths of the Kirchschemmsbach and Haarbach and close downstream from old restored Boye sites, which may have resulted in a more rapid colonisation (de Donnová et al., 2022). Both, the sites LIEohBo and BOYohB224 share some characteristics with standing waters, which is a result from especially low flow velocities in large parts of the streams. Next to the recent restoration measures, this could be another explanation for their different community. The unimpacted and the mature sites did not differ from each other. However, sites from BRA (Brabecker Muehlenbach) were more similar to the Boye and QUAohBo, compared to the other two sites, belonging to the same group. The sites BRAob, BRAohBo and QUAohBo are located close together and have similar environmental conditions, thus offering similar habitats, and ensuring easy access for species from the same source populations. They are located directly upstream of the mature Boye sites, which was also reflected by their community similarity. This shows that the role of colonisation processes may not only differ between maturity stages but may also depend on the sites' location within the stream network (Jones & Schmidt, 2018). Sites that are located close together and therefore well connected, have more similar communities, which are likely controlled by the same filters (Hughes, 2007).

Metacommunity assembly is controlled by different filters, acting in hierarchical order on species level, which were described by Lake et al. (2007). According to them, dispersal determines first, which species can reach the sites, environmental filters dictate whether those species can survive and biotic interactions, such as competition, allow only the strongest competitors to establish a population. To compare the role of the three filters between site groups, we used different metrics per factor, which we calculated for each combination of species and site. We then compared these per site group for present vs. absent species.

### Dispersal filter

We analysed the role of the dispersal filter, using the distances to source populations in the Boye catchment. To this end, we sampled 28 'source' sites, in addition to the 20 'main' sites, and determined per site and species the distance to the nearest upstream source population. The distance to source populations was deemed important for colonisation processes in previous studies (Sundermann et al., 2011; Tonkin et al., 2014). We therefore expected the probability of taxa occurrence to decrease with increasing distance to the nearest source (H2). Consequently, the proportion of taxa present per site should decrease. Our results support our hypothesis. We observed the highest proportion of present taxa to have their nearest source population within a distance of 1.8 km. Beyond this distance, the proportion of present taxa rapidly decreased. Notably, only a relatively small number of cases covered the distance between 0 and 0.5 km, while the highest number had a distance between 0.5 and 1.5 km to the nearest source. This was caused by our sampling design, in which we placed the potential 'source' sites 1 and 2 km upstream of each 'main' site. Upstream 'source' sites closer than 0.5 km were only present, if 'main' sites were located close together and thus serving as 'source' sites themselves for other 'main' sites. The matching of species' occurrences between 'main' sites and upstream 'source' sites is most likely the result from mass effects of the upstream sites, i.e., the massive dispersal of individuals through drift or overland dispersal, which can be initiated by high competition pressure, flood events or mass hatching events (Leibold et al., 2004; Urban et al., 2006). In such cases, environmental conditions of the 'main' sites are less relevant for species to occur, due to continuous influx of new individuals from upstream. If larger distances need to be crossed, environmental conditions at the 'main' site gain importance for long-term establishment, as individuals leaving the site or not surviving cannot easily be replaced by immigrating specimens (Brederveld et al., 2011). A large proportion of absent taxa did not have an upstream source population available, which supports the finding that upstream population sources are a determining factor for species colonisation (Sundermann et al., 2011; Winking et al., 2014; Verdonschot & Verdonschot, 2023). However, a large number but rather low ratio of taxa, was occurring in individual sites despite the absence of a known and sampled source populations. These cases mainly include the unimpacted sites, for which no upstream samples were taken. Due to our sampling design, we may have missed additional source populations, less than 1km upstream. For our analysis, we have only considered upstream source populations. While we assumed this to be the easiest direction of dispersal for benthic invertebrates, dispersal can also be directed upstream, to compensate for aquatic passive downstream drift (Kopp et al., 2001). Especially, taxa with a flying adult stage (Ephemeroptera, Plecoptera, Trichoptera) can easily colonise from neighbouring streams and catchments. In fact, adult caddisflies were reported to fly distances of at least 1.5 km (Graham et al., 2017), although most individuals disperse close to their site of emergence (Collier & Smith, 1998). Passive aerial dispersal is also possible for hololimnic species, e.g., via phoresy (Figuerola & Green, 2002; Van Leeuwen et al., 2013). Hence, taxa could have entered the Boye system from a neighbouring stream network, e.g., the Rotbach or Schwarzbach (Enss et al., 2024). Both streams are in near-natural conditions and could act as potential source populations for the Boye system (Winking et al., 2016).

When comparing the different site groups, we expected that the dispersal filter would constrain taxa from occurring at the recently restored sites (H2). Thus, the present taxa should have a smaller distance to population sources than absent taxa. Distances to population sources differed significantly between present and absent taxa at the recently restored sites. While the same was true for the mature sites, the spread of distances for absent taxa was greater at recently restored sites. In addition, the estimated marginal means were further apart from each other at recently restored sites, compared to the mature sites. This indicates that a dispersal filter is acting on both, the recently restored and the mature sites, albeit stronger on the recently restored sites. Thus, the dispersal filter seem to have a larger role in the early recovery phase, which is in line with the predictions of Vos et al. (2023). In addition to the short time since restoration, this pattern might be increased by the fact that the recently restored sites are all located in the downstream parts of the catchment, further away from potential source sites, which might hamper fast colonization from upstream (compare Li et al., 2018). Taxa that were absent from recently restored sites had a much higher marginal mean than all others, but also distances of present taxa were slightly higher, compared to the mature sites. This indicates that source populations were not as easily available. The smaller difference between absent and present taxa indicates that the mature sites have already been colonised by most of the species occurring in the surroundings. In general, well-connected streams are more readily colonised, compared to unconnected ones (Hughes, 2007). At the unimpacted sites, the distance to the nearest source did not differ significantly between present and absent taxa. Additionally, the marginal mean of present taxa at these sites was higher than that of absent taxa. Upstream sources were unavailable for three of the unimpacted sites, hence the data only results from two sites that are close together, in the upstream part of the catchment. Although anthropogenically affected, these sites were never modified nor used as open sewer. Hence, their longitudinal position and near-natural conditions make them accessible and attractive for dispersing species.

## Environmental filter

Using the habitat suitability calculations, we tested the occurrence of taxa based on the presence of their preferred habitat. We expected that present taxa were characterised by a higher habitat suitability than absent taxa (H3). However, habitat suitabilities evenly ranged from 0.1 to 0.7. The proportion of present taxa increased only slightly towards the end of the gradient, similar to the probability of occurrence. However, at the same time, the number of cases per proportion decreased. Thus, while the general pattern fits our hypothesis, our test was not very strong. The comparison between groups of sampling sites showed that the habitat suitability of absent taxa was lower than that of present species at all sites. Nevertheless, the result was only significant for unimpacted sites. For the mature sites it was only close to significant. Therefore, we found indications that environmental filtering is mainly affecting the unimpacted and, to some degree also the mature sites. Depending on the extent of the restoration measures, existing habitats are removed or severely altered. At the start of the recovery phase, the available habitat is therefore limited. Such conditions allow mainly the occurrence of habitat generalists, resulting in medium habitat suitability values (Winking et al., 2014; Baumgartner & Robinson, 2017). As a result of riparian vegetation growth and organic matter transported from upstream, the habitat heterogeneity increases over time, which results in stronger environmental filtering (Barnes et al., 2013; Liu et al., 2021; Gillmann et al., 2023). Additionally, as previously mentioned, proximity to source populations leads to mass effects, which cause species to colonise less suitable habitats (Leibold et al., 2004). This is especially important in freshly restored streams, where habitats are less readily available, since we observed no significant difference between habitat suitabilities of absent and present taxa. On the other hand, at the mature and unimpacted sites, habitats may have stabilized, facilitating a stable and more specialized community, which translates into higher habitat suitability, especially at unimpacted sites (Gillmann et al., 2023). However, if sites are close together, mature sites may, too, be affected by mass effects from upstream.

In general, our data showed a large mismatch between expected and observed taxa, based on the habitat suitability. This problem was also identified previously in habitat suitability modelling (Brantschen et al., 2024). Presence/absence data might be less indicative for environmental filtering than abundance data because species may be found at less suitable habitats but in lower abundance (Johnson & Vaughn, 1995). Highly suitable habitats would in turn be populated in great numbers. This could also explain the small differences between present and absent taxa per habitat suitability group. Many taxa are not restricted to only one type of substrate, although they may favour some over others. The database freshwaterecology.info accounts for this by defining different affinities to every possible type of substrate. Hence, if a taxon is assigned a low affinity for a certain substrate type, present at the site, the habitat suitability will be lower than if a high affinity for the same substrate is assigned. The taxas' potential to also occur in habitats, not reported by freshwaterecology.info could have also led to the mismatch between the assumed suitability and actual occurrence. In addition, sites within a small catchment, such as addressed here, may not be large enough to exhibit distinct patterns of present and absent species.

### Competition filter

We assessed the role of competition for community assembly, using the Gower similarity index as a measure for trait overlap. To determine if the biotic interaction filter influences the communities of the different site groups, we compared the maximum trait overlap between co-occurring and not co-occurring taxa. As a consequence of competition, we expected the trait overlap between co-occurring taxa to be low, while that of taxa not co-occurring should be high. Accordingly, the proportion of present taxa should decrease with increasing trait overlap.

In contrast to our expectation, the proportion of present taxa was never higher than that of absent taxa, for none of the trait overlap groups. Instead, the proportion of present taxa was always around 40 % across all trait overlap groups. The comparison between site groups did not reveal any significant differences. In contrast to our expectation, the probability of occurrence increased with increasing niche overlap. Only at the unimpacted sites, we observed the trend that present taxa had a lower trait overlap, compared to absent taxa. These results leave do not conclusively resolve our hypothesis since variations in trait overlap were not large enough to show a clear pattern.

Quantifying competition between species is difficult in field studies since trait overlap does not rule out co-existence. The higher similarity between traits of taxa within the same community may result from habitat stabilisation. This aligns with more stable communities that likely prefer similar environmental conditions (Gillmann et al., 2023). Previous studies have shown that the mean trait overlap within restored communities increases with time since restoration, which was defined as an increase in potential interspecific competition (Gillmann et al., 2024). While species with similar traits are more likely to compete with each other, Schlenker et al. (2024) demonstrated that trophic similarity increases over time, indicating that the existing species occupy similar trophic niches. Regional co-existence relies on the local availability of suitable habitats for the competitors. If co-occurring species with high trait overlap are equally good competitors, only the comparison of their abundance will inform, whether one of the populations is suppressed. This could be particularly important on the microhabitat scale. Different patches within the same sampling site can be occupied by different species with similar preferences (Moser & Minshall, 1996). As described by Johnson & Vaughn (1995), densities can identify successful competitors within these patches. Fast reproduction may then be of greater importance than the preferences itself, in order to quickly take up the available niche space. Overall, regional competitive exclusion was previously shown to be a slow process, which can lead to changes in species distributions even if the environmental conditions remain stable (Yackulic, 2017). Thus, trends of increasing and decreasing abundances of possible competitors over time, should be considered for the assessment of competitive interactions within communities.

The lack in differences between trait overlap of co-occurring and not co-occurring taxa could also result from not taking the dispersal filter into account in the first place. From our results, regarding the distance to source populations, we have observed that in many cases, an upstream source population is missing. Other source populations are far away (> 2 km). Hence, only taking taxa with upstream source population into account, could lead to a better explanation of species absences. Species that are not able to reach a respective site, cannot compete with occurring species, making their degree of niche overlap negligible.

## Conclusions

The process of recolonisation is key for the recovery of restored streams. In line with our first hypothesis, the recently restored sites differed from all other sites (H1). Hence, the recolonisation process takes time and is limited by the dispersal filter during early phases of recovery. Early communities consist of species that occur in the close surroundings of the restored sites and therefore strongly depend on nearby source populations (H2). Environmental filtering is especially important in well-developed habitats, where specialised species have established a stable community (H3). We did not observe competition to be important for community assembly (H4). However, competitive exclusion could be important on the microhabitat scale and become more apparent when abundances are taken into account.

Our findings support the assumption that the role of the dispersal and environmental filter differs between different phases of recovery, as proposed by the ARC. Thus, a good connectivity to source populations and support to develop complex habitats during succession are a promising foundation for restored streams to support a diverse benthic invertebrate community. Our results could not support the expected increase in importance of the biotic filter. Thus, future research should be directed at more detailed investigations of interspecific interactions.

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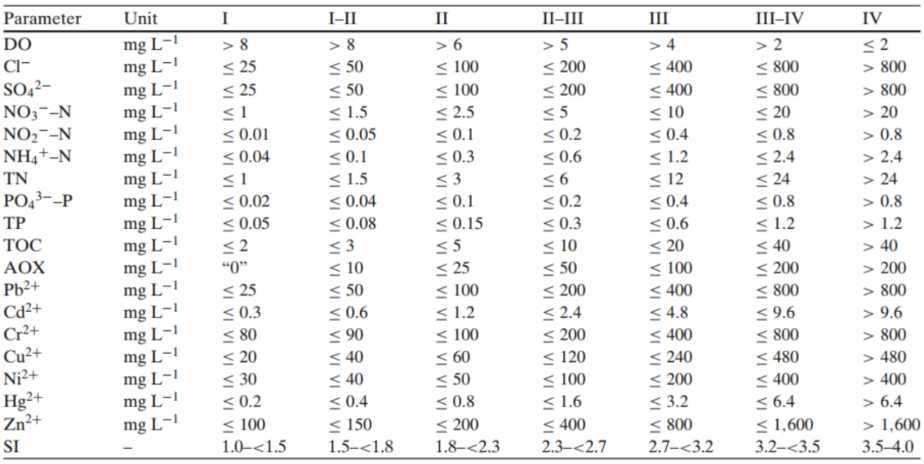
# Supplementary Materials

Appendix S1: Additional information for data processing

Table S1. Eight microhabitat preferences of benthic invertebrates and the corresponding habitat types, as defined in freshwaterecology.info (Schmidt-Kloiber & Hering, 2015)

| Substrate preference | Explanation |
|---|---|
| Argyllal | Silt, loam, clay (grain size < 0.063 mm) |
| Pelal | Mud (grain size < 0.063 mm) |
| Psammal | Sand (grain size 0.063 – 2 mm) |
| Akal | Fine to medium-sized gravel (grain size 0.2 – 2 cm) |
| Lithal | Coarse gravel, stones, cobbles, boulders, bedrock (grain size > 2 cm) |
| Phytal | Algae, mosses, macrophytes |
| POM | Coarse (CPOM) and fine particulate organic matter (FPOM) |
| other | Other substrates |

Table S2. LAWA water quality standards for chemical parameters, and the SI (DEV 1992, 2004; LAWA 1998); published in Bernatowicz et al., 2009.



| Parameter | Unit | I | I–II | II | II–III | III | III–IV | IV |
|---|---|---|---|---|---|---|---|---|
| DO | mg L$^{-1}$ | > 8 | > 8 | > 6 | > 5 | > 4 | > 2 | ≤ 2 |
| $Cl^-$ | mg L$^{-1}$ | ≤ 25 | ≤ 50 | ≤ 100 | ≤ 200 | ≤ 400 | ≤ 800 | > 800 |
| $SO_4{}^{2-}$ | mg L$^{-1}$ | ≤ 25 | ≤ 50 | ≤ 100 | ≤ 200 | ≤ 400 | ≤ 800 | > 800 |
| $NO_3{}^-$–N | mg L$^{-1}$ | ≤ 1 | ≤ 1.5 | ≤ 2.5 | ≤ 5 | ≤ 10 | ≤ 20 | > 20 |
| $NO_2{}^-$–N | mg L$^{-1}$ | ≤ 0.01 | ≤ 0.05 | ≤ 0.1 | ≤ 0.2 | ≤ 0.4 | ≤ 0.8 | > 0.8 |
| $NH_4{}^+$–N | mg L$^{-1}$ | ≤ 0.04 | ≤ 0.1 | ≤ 0.3 | ≤ 0.6 | ≤ 1.2 | ≤ 2.4 | > 2.4 |
| TN | mg L$^{-1}$ | ≤ 1 | ≤ 1.5 | ≤ 3 | ≤ 6 | ≤ 12 | ≤ 24 | > 24 |
| $PO_4{}^{3-}$–P | mg L$^{-1}$ | ≤ 0.02 | ≤ 0.04 | ≤ 0.1 | ≤ 0.2 | ≤ 0.4 | ≤ 0.8 | > 0.8 |
| TP | mg L$^{-1}$ | ≤ 0.05 | ≤ 0.08 | ≤ 0.15 | ≤ 0.3 | ≤ 0.6 | ≤ 1.2 | > 1.2 |
| TOC | mg L$^{-1}$ | ≤ 2 | ≤ 3 | ≤ 5 | ≤ 10 | ≤ 20 | ≤ 40 | > 40 |
| AOX | mg L$^{-1}$ | "0" | ≤ 10 | ≤ 25 | ≤ 50 | ≤ 100 | ≤ 200 | > 200 |
| $Pb^{2+}$ | mg L$^{-1}$ | ≤ 25 | ≤ 50 | ≤ 100 | ≤ 200 | ≤ 400 | ≤ 800 | > 800 |
| $Cd^{2+}$ | mg L$^{-1}$ | ≤ 0.3 | ≤ 0.6 | ≤ 1.2 | ≤ 2.4 | ≤ 4.8 | ≤ 9.6 | > 9.6 |
| $Cr^{2+}$ | mg L$^{-1}$ | ≤ 80 | ≤ 90 | ≤ 100 | ≤ 200 | ≤ 400 | ≤ 800 | > 800 |
| $Cu^{2+}$ | mg L$^{-1}$ | ≤ 20 | ≤ 40 | ≤ 60 | ≤ 120 | ≤ 240 | ≤ 480 | > 480 |
| $Ni^{2+}$ | mg L$^{-1}$ | ≤ 30 | ≤ 40 | ≤ 50 | ≤ 100 | ≤ 200 | ≤ 400 | > 400 |
| $Hg^{2+}$ | mg L$^{-1}$ | ≤ 0.2 | ≤ 0.4 | ≤ 0.8 | ≤ 1.6 | ≤ 3.2 | ≤ 6.4 | > 6.4 |
| $Zn^{2+}$ | mg L$^{-1}$ | ≤ 100 | ≤ 150 | ≤ 200 | ≤ 400 | ≤ 800 | ≤ 1,600 | > 1,600 |
| SI | – | 1.0–<1.5 | 1.5–<1.8 | 1.8–<2.3 | 2.3–<2.7 | 2.7–<3.2 | 3.2–<3.5 | 3.5–4.0 |

Table S3 Borders defined to suit the categories of the species' preferences.

| Trait | Weight | Borders | Source |
|---|---|---|---|
| KLIWA index | 0, 1, 2, 3, 4, 6, 10 | 1, 3, 5, 7, ,9 11, 100 | Sundermann et al. (2022) |
| Saprobic value | 4, 8, 16 | 1, 3, 4 | German saprobic index |
| Flow velocity | - | 0, 0.01, 0.02, 0.05, 0.06, 0.09, 0.1, 0.15, 0.16, 0.25 | STOWA, Verberk et al. (2012) |

Appendix S2. Results of Estimated Marginal Means

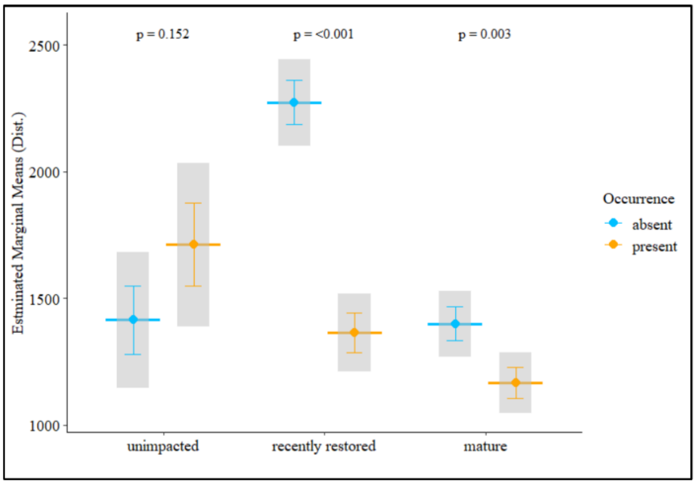


Figure S1. Estimated Marginal Means (EMMs) extracted from GLMM with 'distance to source' as response, 'occurrence' and 'site group' as fixed and 'species' as random effect. Grey vertical bars display the 95% confidence intervals. Horizontal bars depict the EMMs. The difference is statistically different, if standard error bars do not overlap ($p< 0.05$).

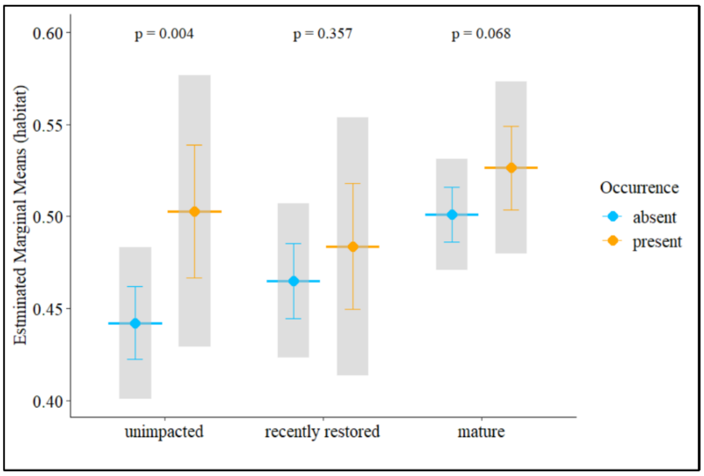


Figure S2. Estimated Marginal Means (EMMs) extracted from GLMM with 'mean habitat suitability' as response, 'occurrence' and 'site group' as fixed and 'species' as random effect. Grey vertical bars display the 95% confidence intervals. Horizontal bars depict the EMMs. The difference is statistically different, if standard error bars do not overlap ($p< 0.05$).

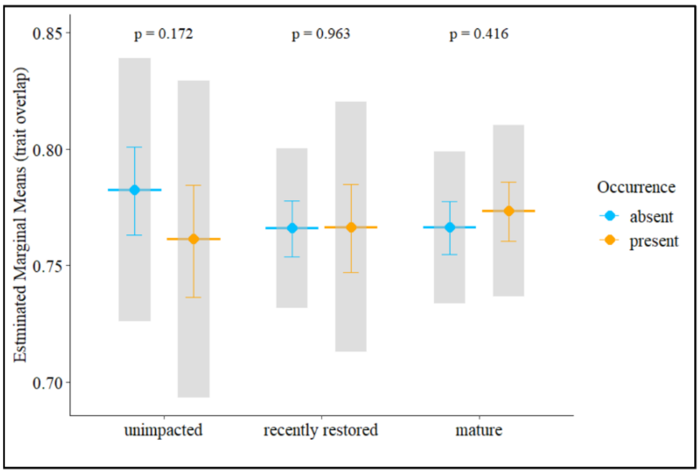


Figure S3. Estimated Marginal Means (EMMs) extracted from GLMM with ‘trait overlap’ as response, ‘occurrence’ and ‘site group’ as fixed and ‘species’ as random effect. Grey vertical bars display the 95% confidence intervals. Horizontal bars depict the EMMs. The difference is statistically different, if standard error bars do not overlap ($p< 0.05$).

## Extent of Contribution

Cumulative thesis of Svenja M. Gillmann

### Author contributions

Title: *Contributions of source populations, habitat suitability and trait overlap to benthic invertebrate community assembly in restored urban streams*

Authors: Gillmann, S.M., Schuwirth, N., Lorenz, A.W. and Hering, D.

Contributions:

- Conception - 70%
- Experimental work/ field sampling - 70%
- Data analysis - 70%
- Species identification - 60%
- Statistical analysis - 100%
- Writing the manuscript - 90%
- Revision of the manuscript - not applicable

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| Unterschrift Doktorand/in | Unterschrift Betreuer/in |

# 4 General Discussion

## 4.1 Summaries of each chapter

The research conducted in this thesis investigated the influence of dispersal, tolerances and competition on recolonisation processes of benthic invertebrates. The first chapter presented a general overview of the patterns of recolonisation following stream restoration, identifying the main environmental drivers. Afterwards, the second and third chapter provided a more detailed examination of the mechanisms underlying the recolonisation process. These chapters showed how the influence of dispersal, tolerances and competition changes throughout the recovery process, varying over time and during different stages of recovery. Summaries of each chapter are provided in the following.

In the first chapter (Gillmann et al., 2023), the general recolonisation patterns of benthic invertebrates were analysed, using abiotic and biotic time-series data collected in 10 consecutive years in restored sites of the Boye catchment. In line with other studies (e.g., Lorenz, 2021), the benthic invertebrate community recovered and stabilized approximately eight years after restoration. Habitats changed from open and gravel dominated, to shaded and sand dominated, which was mirrored by a shift in the corresponding benthic invertebrate community. For example, the good dispersing Mayfly *Cloeon dipterum* and several Coleopteran species were part of the pioneer community, but their abundances quickly decreased over time and other species arrived which preferences suited the developing habitats. Thus, community changes were closely linked to the time since restoration and associated habitat development (Verdonschot et al., 2016). In addition, riparian woody vegetation encroachment over time drove in-stream habitat diversification, supporting species that rely on the allochthonous input of organic matter for food and case building (Palt et al., 2023). Some communities experienced a shift in their composition in response to a severe drought; however, they rapidly recovered to previous conditions. This demonstrates that established communities are more resilient to short-term disturbances (Lake, 2000). These results showed that diverse, stable communities can develop even in previously heavily degraded streams. Time and habitat development are major factors determining community assembly.

In the second chapter (Gillmann et al., 2024a) the assumption of the Asymmetric Response Concept (ARC, Vos et al., 2023) that the importance of the three filters (dispersal, tolerance, competition) changes predictably over time was tested. The analysis was based on similar time-series data as in the previous chapter. Indices were calculated for each of the three filters to analyse their change over time. The communities' dispersal capacity, decreased over time;

pioneer communities consisted of good dispersing generalists and were later joined by slow dispersing specialists. Similarly, the proportion of pollution-tolerant taxa decreased, being replaced by pollution-sensitive taxa. In contrast, no temporal changes of the tolerance toward chloride were observed. Lastly, interspecific competition, measured as trait overlap, increased. The results suggest that dispersal is important for initial colonisation processes, while ongoing improvements of water quality likely led to colonisation of more sensitive species. On the other hand, chloride tolerance was not important, possibly because occurring species were generally tolerant towards salinity, due to the sewage history of the Boye system. The increase in competition was most likely linked to increasing species numbers over time, resulting in higher similarities between species preferences. This study generally supported the hypotheses of the ARC. However, the decrease in tolerance towards organic decomposition contrasted the expectation that stressors are only important prior to recovery. This indicates that prevailing stressors, such as organic pollutants were still present after restoration. Consequently, they continued to influence the benthic community in the recovering system.

In the last chapter (Gillmann et al., 2024b) a site- and species-specific analysis was conducted, to challenge the assumptions of the ARC in regard to the role of the three recolonisation filters (dispersal, tolerance and competition) during different phases of recovery. Compared to the previous analysis the dataset comprised only one year of sampling, but included more detailed information on source populations to quantify the dispersal filter and additional abiotic factors for the tolerance filter, e.g., substrate cover, which were compared to the species' preferences (habitat suitability). The role of the three filters was compared between 'unimpacted' (never restored), 'recently restored' (< 4 years) and 'mature restored' sites (> 10 years). The benthic communities of 'recently restored' sites differed from all other sites. The dispersal filter had the most prominent effect on 'recently restored' sites, and a smaller effect on 'mature restored' sites. The environmental filter was most important at 'unimpacted' sites, less important at 'mature restored' and least important at 'recently restored' sites. Lastly, the biotic interaction filter, i.e., competition, had no effect on any of the site groups. These results supported the dispersal filter to be most important during early recovery, while environmental filtering gained significance over time. Unexpectedly, competition was not important for community assembly, contrasting the results from chapter two. Trait overlap may not be sufficient to determine the role of competition for recolonisation processes. Taxa with similar traits might be able to co-exist within a stream reach, if enough resources are available. On the other hand, they might be competing for space and food on the microhabitat scale, which would not be visible in presence/absence data. Differences in abundance could therefore help to gain further insights.

## 4.2 Long-term community recovery

Outside the scope of this thesis, additional studies investigated the benthic invertebrate community of the Boye catchment (Pimentel et al., 2024; Schlenker et al., 2024). Schlenker et al. (2024) analysed the change in food web composition of benthic invertebrates, using similar time-series data, as the ones in chapter one and two (Gillmann et al., 2023, 2024a). Pimentel et al. (2024) used a mesocosm approach to analyse the influence of reduced flow velocity and enhanced salinity on benthic invertebrates that originated from the Boye catchment. The Boye catchment is exemplary for the recovery section of the ARC (Vos et al., 2023). To gain information on the degradation section of the ARC, temporal changes in community composition of the Kinzig catchment were analysed (Nguyen et al., 2023a, 2023c, 2024; Schürings et al., 2024; Kaijser et al., 2024). The Kinzig catchment covers a degradation gradient, including sites that are near-natural or impacted by urban and agricultural land use. Two studies were focussed on trends of the benthic invertebrate community in the Kinzig catchment alone (Nguyen et al., 2023a, 2023c), while the others included both, the Boye and Kinzig catchment in their analysis (Kaijser et al., 2024; Nguyen et al., 2024; Schürings et al., 2024). Nguyen et al. (2024) used time-series data to analyse the change in community composition, in relation to changes in land use, runoff, precipitation and evaporation and compared them between the Boye- and Kinzig catchment. Schürings et al. (2024) extended the analysis on interspecific competition, conducted in chapter two (Gillmann et al., 2024a) to a nationwide dataset, to analyse the relevance of competition in recovering and degrading systems. Their dataset on recovering systems included the time-series data from the Boye catchment, also used in chapter two (Gillmann et al., 2024a), while the degrading systems included time-series data on the Kinzig catchment. Kaijser et al. (2024) used data, sampled at both, the Boye- and Kinzig catchment, in 2021 and 2022, to analyse the dependence of benthic community structure to gradients of chemical stressors. These additional studies addressing the Boye- and/or the Kinzig catchment have important implications for the results presented in this thesis. In the following, the findings from these studies are discussed in respect to the findings from this thesis and the assumptions of the ARC.

The ARC states that community assembly in systems, impacted by anthropogenic pollution such as the Kinzig catchment is mainly determined by species tolerances (Vos et al., 2023). On the other hand, recovering systems, such as the Boye catchment, are influenced by the interplay of dispersal, tolerances and competition. The importance of each of these factors is expected to change over time (Vos et al., 2023). Indeed, the changes in the benthic communities at sites in the Kinzig catchment (degradation section) were mainly driven by changes in natural and anthropogenic stressor intensity (Nguyen et al., 2024). For example, upstream sites showed larger improvements than downstream sites, due to better water quality upstream and stressors accumulating downstream (Nguyen et al., 2023a). Consequently, downstream benthic communities were characterised by pollution-tolerant species, while pollution-sensitive species were mainly present at the upstream sites. Long-term trends in the benthic invertebrate communities were generally associated with changes in water temperature, land use and runoff (Nguyen et al., 2023c). Compared to the Kinzig catchment, the communities in the recovering Boye catchment exhibited a greater potential for development, due to physicochemical and hydromorphological restoration. They showed more pronounced improvements, due to rapid colonisation of benthic invertebrates following restoration (Gillmann et al., 2023; Nguyen et al., 2024). Community development was closely linked to the time since restoration, during which species numbers gradually increased (Gillmann et al., 2023). While general community improvement was linked to water quality improvement, increase of woody riparian cover (Gillmann et al., 2023) and a shift in land use (Nguyen et al., 2024), initial colonisation was governed by good dispersing species (Gillmann et al., 2023). Over time, community dispersal capacity declined (Gillmann et al., 2024a). Similarly, the distance to source populations was most important for taxa occurring at ‘recently restored’ sites (Gillmann et al., 2024b). Hence, all three chapters of this thesis, showed that dispersal is the most important factor during initial recovery, supporting the ARC. However, the distance to source populations was still important at ‘mature restored’ sites and community dispersal capacity decline was only moderate. Thus, dispersal appears to remain important over longer timeframes, instead of rapidly declining as suggested in Figure 1 (Section 2.4).

Although the ARC assumes species tolerances to not play a role during phases of recovery, water quality improvement facilitated the arrival of more sensitive species in the Boye catchment (Gillmann et al., 2024a). Conductivity decreased over time, but there was no change in the communities’ chloride tolerance (Gillmann et al., 2023, 2024a). While other ions may have been responsible for high conductivity in the streams, mesocosm experiments demonstrated that benthic invertebrates, originating from the Boye catchment, were not affected by salinisation (Pimentel et al., 2024). The history of sewage and mining activities in the Boye catchment may have resulted in chloride-tolerant species assemblages (‘stressor legacy’, Jackson et al., 2021), which stabilise over time (Gillmann et al., 2023). This is further supported by Kaijser et al. (2024), who identified community composition to strongly respond to changes in conductivity. These results demonstrate that stressors and corresponding tolerances are still important during recovery, if the water quality remains impaired. Water quality cannot be expected to return to natural conditions in an instant, even after the main source of pollution has been removed. If the pollutants have settled in the stream sediment, they are continuously washed out due to erosion, causing a retardation of water quality improvement (Glaser et al., 2020). However, the role that these tolerances play for community assembly differs between stressors and depends on stressor intensity. In addition to tolerance toward stressors, tolerances include the species' preferred substrate type. As a result from stream restoration, the instream habitats change and mature over long timeframes (Gillmann et al., 2023). Therefore, natural changes of the streams' surroundings, such as an increasing cover of woody riparian vegetation, can further improve habitat conditions to support more sensitive species assemblages (Gillmann et al., 2023, 2024a, 2024b). A similar pattern was observed at the upstream sites in the Kinzig catchment, where already small water quality improvements and forest land use led to more pollution-sensitive species (Nguyen et al., 2023a). Therefore, increasing habitat quality and stability eventually results in specialised community assemblages (Gillmann et al., 2024b).

According to the ARC, during recovery, the role of biotic interactions for community assembly increases over time (Vos et al., 2023). In this thesis, biotic interactions were analysed in terms of interspecific competition (i.e., trait overlap) in chapter two and three (Gillmann et al., 2024a, 2024b). In the second chapter, competition was found to increase over time (Gillmann et al., 2024a), which correlated with the increase in species richness, described in the first chapter (Gillmann et al., 2023). A similar trend was observed in other recovering catchments (Schürings et al., 2024). Similarly, Nguyen et al. (2024) observed smaller increases in trait than in taxonomic composition, indicating the overlap between traits of newly arriving and already occurring species. These results were contrasted by the findings in chapter three, where trait overlap did not determine species occurrence (Gillmann et al., 2024b). Treating the degree of trait overlap as measure for competition might be too simple, to grasp the complex interactions between species. The accumulation of species with similar traits could be the result from habitat development and stabilisation. Species that are suitable for the given conditions arrive over time and, if resources are not limited, coexist within the respective stream reach (Little and Altermatt, 2018). This is supported by findings from Schlenker et al. (2024), who identified trophic similarity to be correlated to the increase in trait overlap, indicating that the co-occurring species coexist in similar niches. Consequently, competition does not necessarily prevent species with similar traits to colonise the streams (competitive exclusion). Species numbers in the Boye catchment were still low (~30 species per site), compared to near-natural catchments (~50 species per site) (Lorenz, 2021). Therefore, enough niches could still be available for different species to occur, before resources become limited. Competitive exclusion could, however, act on the microhabitat scale. For example, introduction experiments showed competitive exclusion in single patches within streams. Here, recolonisation success depended on the order of arrival (priority effects), competitor identity and the size of the individuals (Eglesfield et al., 2023; Hart, 1983). Additionally, competitive exclusion may occur over much longer timeframes than those observed in this study (Yackulic, 2017). The onset of such processes may already be visible in the population density, which was not included in the second and third chapter. The results show that the role of competition for community assembly should be analysed more thoroughly, which leads to the conclusion that there is still much to recover in this emerging field of science.

# 5 Outlook and Conclusions

## 5.1 Future research

The research conducted in this thesis significantly advances the understanding of recolonisation patterns and the corresponding filters following stream restoration in urban systems. Long-term observations revealed that the benthic community recovered within ten years, despite the history of heavy organic pollution. Recovery was driven by the succession of riparian vegetation and corresponding habitat development. After stable communities developed, they became resilient and recovered quickly from short-term disturbances such as drought (Gillmann et al., 2023). This observation highlights the importance of long-term data for monitoring restored streams. Short-term disturbances can mask restoration effects if not consecutively monitored, which is particularly relevant in the context of climate change, causing extreme weather events to occur more frequently. Only consecutive long-term data, collected over many years, allows to observe the complex patterns of metacommunity assembly during the process of recovery. This can help to improve management efforts and reveals, whether communities could indeed recover, or recovery is prevented by biotic misfunctions or the presence of abiotic pressures. The increasing frequency of heatwaves, resulting in drought, further raises the need to investigate the patterns of recolonisation after complete streambed drying. The mechanisms of recovery may differ from those, following stream restoration, which could be important to predict how benthic communities will cope under future conditions.

During recovery, the benthic community followed a specific pattern that was mostly in line with the assumptions of the ARC. In all chapters the importance of dispersal and environmental improvements for successful recovery of benthic invertebrate communities was highlighted. Patterns of interspecific competition, however, were contradicting, raising the need for different methods to quantify competition and the role of competitive exclusion for community assembly. As described in section 4.2, the use of trait overlap alone does not seem to be sufficient to estimate the degree of competition between species. Many species are not restricted to one food source or one habitat but have preferences for different food sources and habitats; hence, trait overlap does not necessarily mean that they compete with each other within a stream reach. Even if co-occurring species rely on similar resources, these are not necessarily limited within the stream reach. Instead, competitive exclusion was suggested to play a role on the microhabitat scale, making it necessary to study community dynamics within single patches of a stream (Eglesfield et al., 2023). A possible consequence of competition is the decreasing abundance of the weaker competitor. Thus, a small-scale investigation of single stream patches could possibly be avoided by analysing changing abundances of co-occurring species with similar preferences over time. This might provide a more realistic representation of competitive interactions. Including isotopic methods to measure the trophic similarity between potentially competing species could further enhance the results, because high competition pressure could force one of the competitors to switch food sources.

In chapter three of this thesis (Gillmann et al., 2024b), a space for time approach was used to compare the role of each colonisation filter between stages of recovery. This study could be extended by including upstream dispersal into the analysis, because merolimnic species are known to compensate for downstream drift by active upstream dispersal (Kopp et al., 2001). Additionally, the main study sites are part of an annual monitoring program, making it possible to include the community composition of the following years in further analyses. These could be used to investigate whether species originating from distant population sources migrate into the restored sites over time. The distance to population sources could further be related to the different dispersal capacities, to test the assumption that good dispersers reach distant sites more quickly than weak dispersers.

This thesis mainly focussed on a single aquatic organism group of a single urban stream catchment, which has the special history of being used as open sewer for almost a century. Therefore, the patterns of benthic invertebrate recolonisation, observed in this thesis, are likely to differ from those in more natural catchments and without an extreme pollution history. For example, catchments colonised by more species-rich communities might be more resistant or resilient to recolonisation. The methods used here should therefore be extended to other restored catchments. In addition, the mechanisms acting during recolonisation should be tested for other biotic indicators, e.g., phytobenthos and fish, as they might have different requirements for successful recovery.

## 5.2 General conclusions

The results presented in this thesis demonstrate that even streams that have been heavily degraded, with a history as open sewer, can recover and support stable, diverse benthic communities. The recolonisation processes followed a distinct pattern, with dispersal and environmental improvements being most important. These findings are especially relevant for urban streams, because recolonisation patterns will likely differ from those in more natural catchments. Restoration efforts of urban streams are often limited to the available space, restricted by anthropogenic structures, and by prevailing stressors. Additionally, source populations are often more limited, compared to catchments surrounded by grassland and forest land use. To overcome these challenges, future planning of conservation and restoration strategies of urban streams should consider the recovery trajectories, proposed by the ARC; with primary focus on maintaining or improving the local habitat, while considering potential dispersal pathways. The recolonisation patterns, observed in this thesis, can help stream managers, to determine the recovery status of urban streams and to identify barriers that interrupt the recolonisation processes.

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## Curriculum vitae

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# Declarations

### Declaration

In accordance with § 6 (para. 2, clause g) of the Regulations Governing the Doctoral Proceedings of the Faculty of Biology for awarding the doctoral degree Dr. rer. nat., I hereby declare that I represent the field to which the topic "*Colonisation patterns and -mechanisms of riverine benthic invertebrate communities following restoration of urban streams"* is assigned in research and teaching and that I support the application of Svenja M. Gillmann.

Essen, date ________________ ________________________________________________

Name and Signature of the scientific supervisor/member
of the University of Duisburg-Essen

### Declaration

In accordance with § 7 (para. 2, clause d and f) of the Regulations Governing the Doctoral Proceedings of the Faculty of Biology for awarding the doctoral degree Dr. rer. nat., I hereby declare that I have written the herewith submitted dissertation independently using only the materials listed, and have cited all sources taken over verbatim or in content as such.

Essen, date _________________ ________________________________________________

Signature of the doctoral candidate

### Declaration:

In accordance with § 7 (para. 2, clause e and g) of the Regulations Governing the Doctoral Proceedings of the Faculty of Biology for awarding the doctoral degree Dr. rer. nat., I hereby declare that I have undertaken no previous attempts to attain a doctoral degree, that the current work has not been rejected by any other faculty, and that I am submitting the dissertation only in this procedure.

Essen, date _________________ ________________________________________________

Signature of the doctoral candidate