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Alteration of physico-chemical and microbial properties in freshwater substrates by burrowing invertebrates

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ABSTRACT

The hyporheic interstitial provides habitat for many different organisms – from bacteria to burrowing invertebrates. Due to their burrowing and sediment reworking behaviour, these ecosystem engineers have the potential to affect hyporheic processes such as respiration and nutrient cycling. However, there is a lack of studies that characterize the interactions between bioturbators, physico-chemical habitat properties and microbial communities in freshwater substrates. In a standardized laboratory experiment, we investigated the effects of three functionally different bioturbators, duck mussels (*Anodonta anatina*, Linnaeus 1758), mayfly nymphs (*Ephemera danica*, Müller 1764) and tubificid worms (*Tubifex tubifex*, Müller 1774), on the physico-chemical conditions and bacterial communities in hyporheic substrates. We hypothesized that different invertebrates distinctly alter habitat conditions and thus microbial community composition, depending on the depth and the manner of burrowing. *A. anatina* and *E. danica* caused an increase in interstitial oxygen concentration, whereas strong declines in oxygen concentration and redox potential were detected in the *T. tubifex* treatment. These effects on physico-chemical habitat properties were even detectable in open water. Mussels and tubificid worms also significantly influenced the composition of bacterial communities in the hyporheic zone. A loss or replacement of bioturbators in stream ecosystems due to anthropogenic habitat alterations is expected to result in shifts in microbial community compositions, with effects on nutrient fluxes, pollutant degradation and benthic food webs. An understanding of the effects of functionally different native and invasive bioturbators is crucial to predict changes in stream ecosystem functioning.

1. Introduction

The hyporheic zone is closely linked with ecosystem functions and services (Geist 2014). Due to its heterogeneity, it provides a variety of microhabitats inhabited by microscopic and macroscopic organisms (Braun et al., 2012; Lowell et al., 2009) such as the larvae of unionoid freshwater mussels (Geist, 2010), Ephemeroptera (de Haas et al., 2005; Percival and Whitehead, 1926; Stief et al., 2004) and Oligochaeta (Mermillod-Blondin et al., 2001; Pelegri and Blackburn, 1995). Species inhabiting the hyporheic zone change their environment and as such alter substratum conditions. Bioturbating mussels or insect larvae burrow into the sediments and may therefore increase oxygen and nutrient exchange rates between open and interstitial water (de Haas et al., 2005; Howard and Cuffey, 2006; Vaughn and Hakenkamp, 2001). Benthic invertebrates can also influence the structure and physico-chemical conditions of the hyporheic zone (Mermillod-Blondin et al., 2001; Navel et al., 2012; Nogaro et al., 2006; Stief et al., 2004). Such alterations have the potential to influence microbial communities, which are likely the most important organisms of the hyporheic zone (Baerlocher et al., 2006; Cornut et al., 2010; Febria et al., 2011; Lowell et al., 2009), as they are the actual drivers of decomposition of organic material, nutrient turnover and pollutant degradation (reviewed in Marmonier et al., 2012).

Depending on their life style and burrowing behaviour, different ecosystem engineers can be expected to distinctly alter habitat properties. Gardner et al. (1987), François et al. (1997, 2002) and Gerino et al. (2003) defined five functional groups of substrate

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reworking organisms: biodiffusors, upward conveyors, downward conveyors, regenerators and gallery diffusors. The species chosen in this study represent three of those functional groups. *A. anatina* acts as a regenerator causing sediment redistribution and creating open burrows by moving horizontally on the sediment as well as vertically in and out of it (Amyot and Downing, 1998; Zieritz et al., 2014). The burrows of indigenous European mussels can be up to 20 cm deep (Schwalb and Pusch, 2007). Inhabiting the top centimeters of stream substrata, larvae of the mayfly *E. danica* act as biodiffusors, causing omnidirectional substratum movements on the surface of streambeds. The hemimetabolic Ephemeroptera burrow U-shaped tubes of about three cm depth (Winkelmann and Koop, 2007), where they perform wavelike movements to filter food, such as detritus and algae (de Haas et al., 2005). *T. tubifex* belongs to the upward-conveyor group, feeding on sediment at depth and ejecting faecal pellets at the sediment water interface (Nogaro et al., 2009). In addition to sediment, tubificid worms also feed on detritus in the upper two to eight centimeters of the substratum (Pelegri and Blackburn, 1995). Due to the smaller diameter of *T. tubifex*, their burrows are smaller than those of Ephemeroptera, however, *T. tubifex* can reach higher densities up to 70,000 individuals per m^2 (Pelegri and Blackburn, 1995).

Much is known about hyporheic physical characteristics at the reach scale (Baker et al., 1999; Morrice et al., 1997), which is the basis for understanding hyporheic functioning. In contrast, knowledge about local interactions between abiotic and biotic drivers is scarce but necessary to explain the functioning of the whole hyporheic ecotone. Marmonier et al. (2012) identified many gaps in the current understanding of the dynamics of benthic invertebrate communities. To date, only few studies have specifically investigated the impact of invertebrates on microbial activity and processes (Mermillod-Blondin et al., 2001, 2003). In particular, the interactions between burrowing organisms, streambed conditions, microbial diversity and biogeochemical processes are still unclear (Boulton, 2000; Marmonier et al., 2012). Microorganisms in the hyporheic zone influence the physico-chemical conditions and, in turn, their activity and diversity depend on those conditions (Navel et al., 2011, 2012; Stief et al., 2004).

The present study allows direct comparisons of the effects of functionally different bioturbators with a focus on the interaction between burrowing invertebrates, substratum conditions and bacterial diversity in the hyporheic zone. A standardized laboratory mesocosm experiment was set up with different macroinvertebrates and a control without organisms. Physico-chemical habitat properties and microbial diversity were analyzed in a multivariate statistical approach. The aims of the study were to evaluate the effects of three functionally different (size, burrowing depth, burrowing style) macroinvertebrates (*E. danica*, *T. tubifex* and *A. anatina*) on physico-chemical parameters expected to be crucial for microbial diversity (pH, oxygen concentration and saturation, electric conductance, redox potential and N-cycle related ions) in the interstitial and open water. Moreover, differences in microbial community composition in the presence of burrowing organisms were assessed. We hypothesized that (i) the analyzed organisms modulate physico-chemical conditions in the interstitial and open water distinctly which should be reflected in (ii) different microbial community composition in the presence of *E. danica*, *T. tubifex* and *A. anatina* versus the control, respectively. From results of Vaughn and Hakenkamp (2001), we expected the mussels to alter habitat conditions in the direction to an oxygen-rich environment possibly leading to a microbial community dominated by obligate aerob or at least facultative aerob bacteria. The same was expected for the mayfly nymphs due to the findings of Wang et al. (2001) but to a lesser extent because of the smaller burrows of the insect larvae compared to those of the bivalves. The reported effects of tubificid worms reach from oxygen increase (Mermillod-Blondin and Lemoine, 2010) to oxygen decrease in substratums (Nogaro et al., 2007). We expected a slight oxygen decrease due to the deposition of faecal pellets probably resulting in high amounts of oxygen-consuming feces-degrading bacteria.

In a standardized laboratory experiment, the effects of mayfly nymphs (*E. danica*), tubificid worms (*T. tubifex*) and duck mussels (*A. anatina*) on temperature, pH, oxygen concentration and saturation, redox potential, electric conductance and microbial community composition were investigated.

2. Material and methods

2.1. Study design

Plastic boxes (24.2 × 15.5 × 18.2 cm, Rotho Kunststoff AG, Würenlingen, Switzerland) were filled with a 10.0 cm substratum layer and randomly placed (Balanced latin square scheme, Evans, 1976) in three glass-fibre reinforced plastic-channels (3.55 × 0.45 × 0.17 m, AGK Kronawitter GmbH, Wallersdorf, Germany) for 35 days (Fig. 1a). Each box was filled with defined grain fractions (0.85, 0.63 and 0.063 mm in a proportion of 1.5:0.5:4.0) of washed and dried (100 °C) substratum from the Moosach River (a calcareous river, 48° 23′ 39.22′N; 11° 43′ 26.65′E) and constantly supplied with filtered water (mesh width 500 μm, Aquacultur Fischtechnik GmbH, Nienburg, Germany) from a drip-system from the same river with a flow rate of 3.5–4.0 l/h

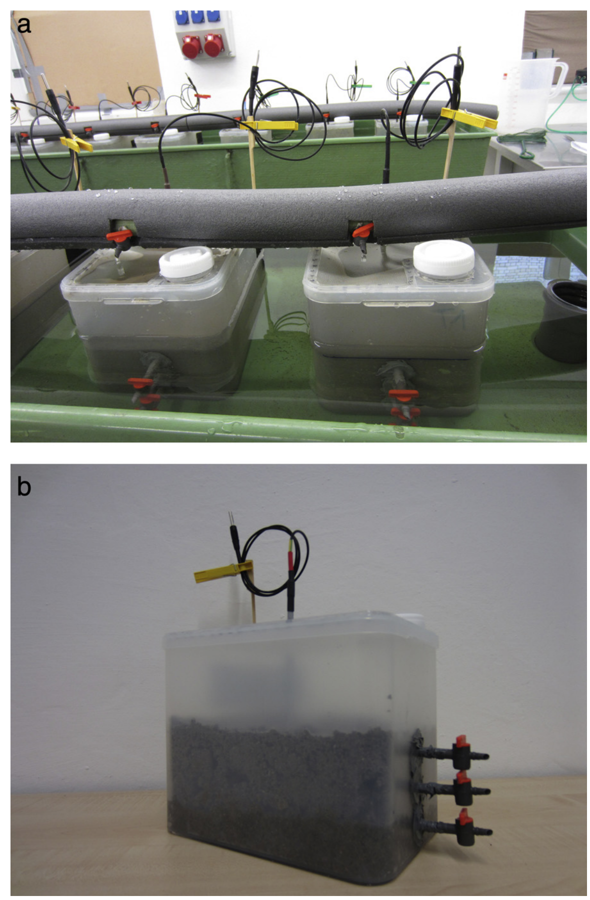

Fig. 1. (a) Photograph of two substratum-filled experimental boxes constantly supplied with natural water from the Moosach River using a drip-system and placed in a glass-fibre reinforced plastic-channel filled with overflowing water from the experimental boxes. (b) Photograph of a substratum-filled experimental box equipped with a lid of gauze (to prevent the test animals from escaping), an installed redox electrode for measuring the interstitial redox potential, and three control valves to collect water samples from the substratum.