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Original research article

Is the unsaturated sediment a neglected habitat for riparian arthropods? Evidence from a large gravel-bed river☆

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HIGHLIGHTS

- Unsaturated river sediments below the surface and above the groundwater are unexplored.
- We developed and deployed novel tube traps to study subsurface arthropod assemblages.
- Abundant and diverse arthropods used the entire unsaturated zone down to 1.1 m depth.
- We hypothesize on possible functions of this zone for arthropod population dynamics.
- Unsaturated sediments are likely the most extensive albeit neglected habitat along braided rivers.

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ABSTRACT

Despite exposed surface sediments of braided, gravel-bed rivers host a diverse and endangered arthropod fauna, the ecology of the unsaturated layers below the surface but above the groundwater is mostly unexplored. Even if only parts of this zone are accessible to arthropods, this could be the most extensive habitat along braided rivers with likely important functions for arthropods' population dynamics. Across a 200 m-wide gravel bar at the Tagliamento River (Italy), we investigated the abundance, taxon richness, and composition of arthropods at varying sediment depth (0, 0.1, 0.6 and 1.1 m), distance from the channel (1, 5, 20, and 60–100 m), and time of the year (February–November). We used conventional pitfall traps and novel tube traps to sample surface and subsurface sediments comparably. Although abundance and diversity hotspots were located at the sediment surface at the edge of the gravel bar, the subsurface sediments supported an abundant arthropod fauna with similar richness to the sediment surface. We demonstrate that arthropods inhabit unsaturated sediments throughout the year, and speculate on the zone's role as refugium and/or partial habitat. To ensure the future of this dynamic and diverse habitat we urge science, conservation, and management to include it in future programmes.

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☆ Author Contributions: SDL and KT conceived and designed the experiments, SDL conducted fieldwork, SDL analysed the data and performed statistical analyses. SDL and KT wrote the manuscript.

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1. Introduction

Over the past two centuries braided, gravel-bed river floodplains became among the most threatened ecosystems worldwide, experiencing a major decline in biodiversity caused by habitat alteration, flow and flood control, invasion by exotic species, and pollution (Caruso, 2006; Habersack and Piegay, 2008; Tockner and Stanford, 2002). Naturally, braided gravel-bed rivers feature a dynamic mosaic of aquatic and terrestrial habitats (Tockner and Stanford, 2002). The most extensive habitat along braided rivers is composed of extensive patches of poorly vegetated gravel, usually exposed to the air (aka exposed riverine sediments, ERS; Bates et al., 2009). Due to fluctuations in discharge, the area of these exposed sediments expands and contracts. However, some sediments are exposed for most of the time up to flows approaching bank-full. The harsh disturbance regime along gravel-bed rivers means that exposed sediments are characterized by high turnover rates, low primary productivity and large temperature fluctuations (Bates et al., 2009; Langhans et al., 2008). Along the Tagliamento River (NE Italy), for instance, summer temperature at exposed sediment surfaces can vary from 10 °C in the night to more than 40 °C during the day (Tonolla et al., 2010).

The physical extremes mean that arthropods occupying exposed riverine sediments tend to be highly specialized and rare (Andersen and Hansson, 2005; Bates et al., 2009). In the UK, for example, 489 beetle species were found at 69 ERS sites, 81 species of which (17%) had conservation status (i.e. vulnerable, rare or nationally scarce, defined after Hyman, 1992, 1994; Sadler et al., 2004). Since exposed sediments sit within a mosaic of riverine habitats, which foster a high beta and gamma diversity on these gravel surfaces, they are hotspots of biodiversity (Andersen and Hansson, 2005; Datry et al., 2014; Naiman et al., 1993; Ward, 1998). Along the Tagliamento River, bare and vegetated exposed sediments provided habitat for more than 1000 beetle species, almost half of which had a high fidelity to rivers (Kahlen, 2003, 2009).

Despite the importance of gravel-bed rivers in general, and exposed riverine sediments in particular, the ecology of the unsaturated layers below the surface but above the groundwater has remained almost totally unstudied to date. We are aware of only a single preliminary study that has focused on this habitat explicitly. Dieterich (1996) exposed sediment cages within a gravel bar of the Isar River in Germany and discovered a diverse invertebrate assemblage comprising both aquatic (Oligochaeta, Diptera and Trichoptera larvae) and terrestrial (Acari, Staphylinidae, Carabidae) groups. Arthropods may actively use unsaturated sediments to shelter from harsh environmental conditions. Ambient temperature, for instance, can drop from 46 °C on the surface to 30 °C within the first 12 cm of the sediment (Tonolla et al., 2010). When there are no alternative means of escape or avoidance, some arthropods can survive inundation within the sediment refugium for hours or days (Andersen, 1968; Hammond, 1998). As the volume of the unsaturated sediments expands and contracts with changing water level, their use may be limited to highly mobile arthropods that are able to respond to rapidly changing conditions. The unsaturated sediments are thus an important part of the overall habitat of arthropods found on/in riverine gravels. Knowledge of all the essential partial habitats riparian arthropods depend on is important for understanding population dynamics and informing science-based management and conservation.

Extensive layers of unsaturated sediments are a key feature of braided gravel-bed rivers. Along the Tagliamento River in Italy, for example, the 38.7 km^2 of sediments exposed at base flow are associated with approximately 58 $\times$ 10^6 m^3 of unsaturated sediments, if we assume their average depth to be 1.5 m. Hence, even if only parts of the unsaturated sediments are accessible to arthropods, this is likely the most extensive habitat along braided rivers, and thus of great importance for arthropod population dynamics and ecosystem processes.

Most sampling of riparian arthropods relies on surface hand searching methods and pitfall trapping (Corti et al., 2013; Sadler et al., 2004), which collect sub-surface arthropods relatively poorly. To address this methodological limitation, we designed a comparative field study using conventional pitfall traps on the sediment surface, and novel tube traps deployed within the sediment to study surface and subsurface arthropod assemblages concurrently. We hypothesize that unsaturated sediments are key habitats for arthropods, and that they use them depending on (i) depth, (ii) the location across the gravel bar, and (iii) time of the year. Based on our findings, we discuss the functional importance of the unsaturated sediments for riparian arthropod population dynamics.

2. Material and methods

2.1. Study area

The Tagliamento River is one of the last near-natural river corridors in the European Alps (Tockner et al., 2003). It originates in the southern fringe of the Alps (Italy), and flows south to the Adriatic Sea with very little channel or flow manipulation. The braided middle reach, which we studied, contains a spatially complex and temporally dynamic habitat mosaic dominated by extensive gravel bars, which are separated by river channels and vegetated islands (Petts et al., 2000), and fringed by a ribbon of intact riparian forest (Fig. 1(a)). These channels can fall dry at the surface during low flow conditions, exposing large areas of riverine sediments (Doering et al., 2007). Discharge peaks usually occur in spring and autumn, although flow/flood pulses and dry spells may occur at any time of the year (Tockner et al., 2003, Tab. 1).

We selected a four ha large gravel bar (46°12′6.10″ N, 12°58′7.99″ E; maximum length = 0.37 km; maximum width = 0.24 km), which was bordered on the left side by a 20 m-wide channel, and on the right bank by a small side channel (width $\leq$ 5 m) and the riparian forest (Fig. 1(a)). Sediments on the gravel bar consisted of gravel and pebble (Tockner et al., 2003) with patches of sand along the side channel (Tab. S1, Appendix A).

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