Global Ecology and Conservation 2 (2014) 129–137

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: www.elsevier.com/locate/gecco

Original research article

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

Simone D. Langhans[a,b,*], Klement Tockner[a,b,c]

[a] Eawag, Swiss Federal Institute of Aquatic Science and Technology, Überlandstrasse 133, 8600 Dübendorf, Switzerland
[b] Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310, 12587 Berlin, Germany
[c] Institute of Biology, Freie Universität Berlin, 14195 Berlin, Germany

## 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.

## ARTICLE INFO

*Article history:*
Received 21 July 2014
Received in revised form 29 August 2014
Accepted 29 August 2014
Available online 16 September 2014

*Keywords:*
Conservation
Exposed sediments
Gravel-bed river
Refugium
Tagliamento River

## 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.


☆ 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.
* Corresponding author at: Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310, 12587 Berlin, Germany. Tel.: +49 0 30 641 81 618; fax: +49 0 30 641 81 750.
*E-mail addresses:* simone.langhans@gmail.com, langhans@igb-berlin.de (S.D. Langhans).

http://dx.doi.org/10.1016/j.gecco.2014.08.009

## 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 ≤ 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).

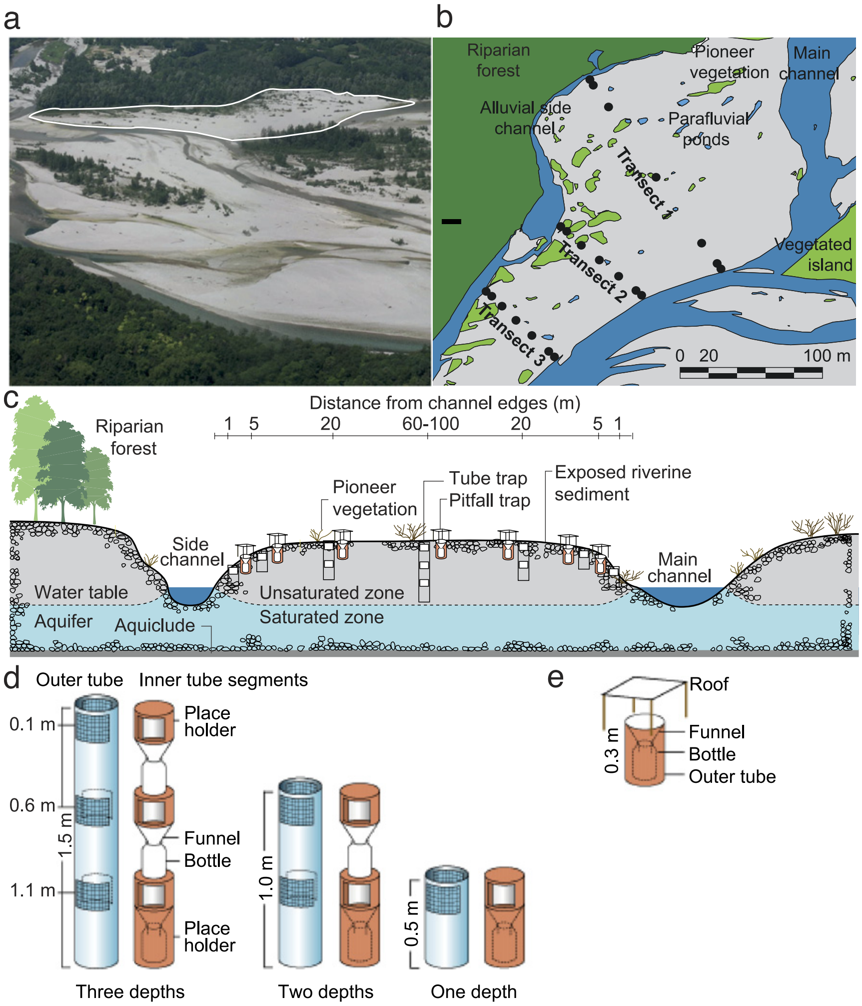


**Fig. 1.** The island-braided reach of the Tagliamento River (sampled gravel bar encircled, river flow from right to left; (a), aerial view of the three transects across the gravel bar (b), a schematic cross-section of a transect (c), tube traps used to collect arthropods in the unsaturated sediments (d), and pitfall traps used to collect arthropods on the sediment surface (e). We show outer and inner tube segments separately for illustration purposes.

## *2.2. Transects and trapping of arthropods*

We sampled arthropods at the sediment surface (0 m), and at three depths within the sediment (0.1, 0.6, and 1.1 m) at seven locations along each of three transects. The seven locations extended from one channel edge to the opposite edge close to the riparian forest at 1, 5, and 20 m from the main channel's edge, in the middle of the gravel bar (approx. 60–100 m from both channel edges, respectively), and 20, 5 and 1 m from the side channel's edge (Fig. 1(b), (c)). Transects were installed at 60 m distance to minimize dependency effects.

We used two trapping methods: (i) Tube traps (modified after Dieterich, 1996) for quantifying the density of arthropods in the unsaturated sediments (Fig. 1(d)), and (ii) conventional pitfall traps to collect arthropods at the sediment surface (e.g. Corti et al., 2013) (Fig. 1(e)). Each tube trap consisted of an outer plastic tube (inner Ø = 15 cm) with square, trellised holes (20 cm × 12 cm, mesh size = 1 cm), and enclosed inner tube segments (outer Ø = 15 cm) with each consisting of a place holder with two opposite openings (20 × 12 cm) and a sampling device composed of a white funnel attached to a white plastic bottle (250 ml, 70% ethanol). We adjusted the length of the trap and therewith the number of inner tube segments (one to three) to the level of the groundwater table, which changed along the sampling transects (Fig. 1(c)).

Pitfall traps measure activity density rather than true abundance (Baars, 1979; Luff, 1975), but are considered an efficient standard sampling method in terrestrial ecology (Spence and Niemela, 1994). Tube traps similarly measure activity density in the unsaturated sediments, as they rely on the movement activity of arthropods to lead to capture. Therefore, both trap types are efficient for capturing active arthropods like beetles, but not for defining the whole arthropod fauna.

At each of the seven sampling locations along each transect, we installed tube traps and pitfall traps in pairs (Fig. 1(c)) four months before the experiment to diminish disturbance effects on the fauna.

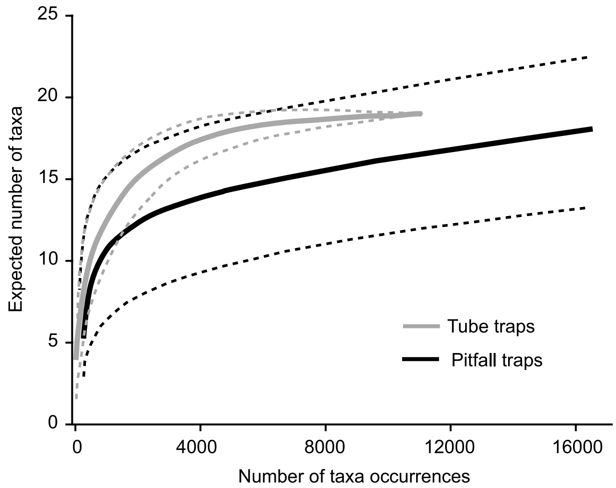


**Fig. 2.** Rarefaction curves for pitfall traps (sediment surface) and tube traps (unsaturated sediments) scaled to the number of occurrences. The dotted lines indicate the 95% CI (tube trap samples: $N = 319$; pitfall trap samples: $N = 210$).

### *2.3. Sampling scheme and arthropod identification*

Each month from February 2005 until November 2005, pitfall traps were exposed for approximately one week (mean exposure duration ± SD: 7.6 days ± 1.17) and tube traps for approximately two weeks (13.5 days ± 2.55). The tube traps were exposed for longer time periods to compensate for the expected lower abundances in the unsaturated sediments. To avoid flooding of the traps, sampling duration differed among months.

Samples were sieved through a 100 μm-mesh screen in the laboratory, and the retained arthropods were sorted to the level of order, subclass, or subphylum (Tab. S2, Appendix A) and counted. For the purpose of our study — the exploration of the unsaturated zone as a potential habitat for riparian arthropods — a coarse taxonomic resolution was considered appropriate (Beattie and Oliver, 1994).

### *2.4. Data analyses*

To calculate an index of arthropod density, catch data (individuals) were converted to units, based on the area of the opening of each trap type and the exposure time (i.e., N $m^{-2}$ $day^{-1}$, hereafter called arthropod abundance). The area of the opening for tube traps was the sum of the two opposite square holes (0.048 $m^2$) (Fig. 1(d)), and for pitfall traps the circular opening area of the funnel (0.018 $m^2$) (Fig. 1(e)). Richness was calculated as the number of taxa per replicated location. Since exposure duration of the two trap types differed, we computed and graphically compared the estimated total taxa richness of the two trap types, using the mean Chao1 estimator of the EstimateS software (vers. 9.0; Colwell, 2013).

To test for similarity in sampling efficiency between pitfall and tube traps, we used rarefaction (*sensu* Gotelli and Colwell, 2001). We computed sample-based rarefaction curves with 95% confidence intervals (CI) (EstimateS vers. 9.0) using 100 iterations without replacement, which we rescaled to the number of occurrences (instead of number of individuals) because datasets differed in the mean number of individuals per sample (Gotelli and Colwell, 2001). We compared the rarefaction curves of the two methods graphically (Fig. 2) and considered them similar, since the 95% CIs overlapped (Colwell et al., 2012; see also Corti et al., 2013, for an application). This signifies that pitfall- and tube traps feature comparable sampling efficiency, and catches could be further analysed concurrently (Ellison et al., 2007; Gotelli and Colwell, 2001; Longino et al., 2002). One has to keep in mind, however, that the difference in habitat permeability between the unsaturated sediments and the sediment surface may have biased activity density in the two habitats (see discussion below).

We evaluated the effect of vertical and lateral floodplain gradients (fixed factors) on patterns of relative arthropod abundance and richness (dependent variables) over time (random factor), applying linear mixed models (LMMs; SPSS ver. 19.0/SPSS Inc., Illinois, USA) for each dependent variable separately. We chose LMMs as they can handle correlated residual errors (e.g., due to repeated sampling), unequal variances, unbalanced designs, and missing values; all of which were issues in this study. Missing values occurred in February (two samples), April (two samples), and May (seven samples) when individual traps within the sediment were flooded.

The vertical gradient consisted of four levels including the sediment surface (0 m), and 0.1, 0.6 and 1.1 m depth (Fig. 1(c)). The lateral gradient comprised four levels, each one representing a specific distance from the channels' edges (1, 5, 20 and 60–100 m) (Fig. 1(b), (c)). The temporal gradient spanned ten months from February to November.

Differences in relative arthropod abundance and richness among the different levels within the gradients were examined using Bonferroni post-hoc tests. Model parameters (fixed effects and variance components) were estimated using the restricted maximum likelihood method with a first-order, autoregressive covariance matrix that fitted our data best

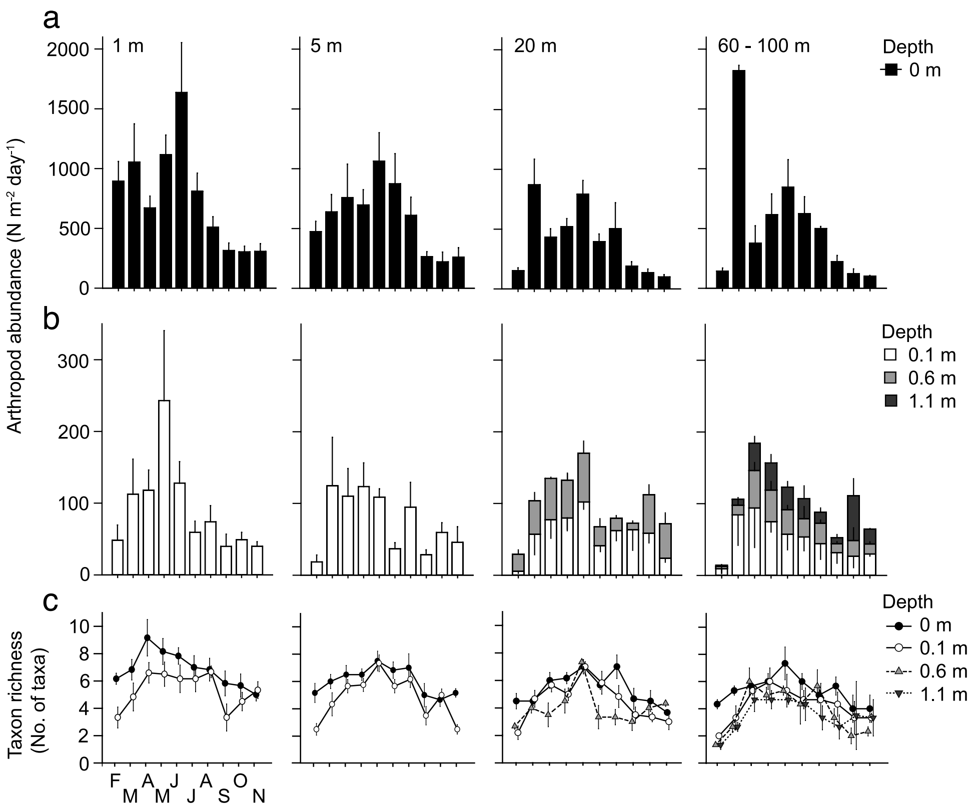


**Fig. 3.** Monthly changes in arthropod abundance (N $m^{-2}$ $day^{-1}$; a and b) and taxon richness (no. of taxa; c) at four different depths (0 = black bars and symbols, 0.1 = open bars and symbols, 0.6 = light grey bars and symbols, and 1.1 m = dark grey bars and symbols), and at four distances across a large gravel bar (1, 5, 20, and 60–100 m distance from the channel edges) (mean +/− SE; $N = 3$–6).

(determined by Akaike's information criterion). We considered catches within sites to be independent, given the small surface of each trap compared to the investigated area. Significance levels were set at $P \leq 0.05$.

## 3. Results

### 3.1. Arthropod abundances

At the sediment surface, arthropod abundance ranged from 205.4 ± 34.7 N $m^{-2}$ $day^{-1}$ (November) to 1118.7 ± 155.2 N $m^{-2}$ $day^{-1}$ (June) (mean ± 1SE: 638 ± 37 N $m^{-2}$ $day^{-1}$, $N = 210$), whereas in the unsaturated sediments (pooled depths) it ranged from 19.8 ± 5.3 N $m^{-2}$ $day^{-1}$ (February) to 108.3 ± 24.8 N $m^{-2}$ $day^{-1}$ (May) (mean ± 1SE: 65 ± 5 N $m^{-2}$ $day^{-1}$, $N = 330$).

Arthropod abundance varied significantly with depth ($F_{3,150.5} = 71.6$, $P < 0.001$), lateral distance across the gravel bar ($F_{3,148.6} = 6.0$, $P = 0.001$), and with time ($F_{9,324.5} = 10.4$, $P < 0.001$) (Fig. 3(a), (b)). Throughout the entire sampling period, significantly more arthropods were captured from the sediment surface than the subsurface sediments (Fig. 3(a)). In the subsurface sediments, arthropod abundance decreased with increasing depth; however, these differences were not statistically significant (Fig. 3(b)). Across the gravel bar, abundances were significantly higher close to the channels (1 and 5 m distance) than at 20 and 60–100 m distance from channel edges (Fig. 3(a), (b)). During the ten months of the study, the lowest abundances were recorded in November (mean ± 1SE: 101 ± 18 N $m^{-2}$ $day^{-1}$, $N = 54$), and the highest abundances in May (mean ± 1SE: 487 ± 92 N $m^{-2}$ $day^{-1}$, $N = 54$) (Fig. 3(a), (b)).

### 3.2. Arthropod richness

At the sediment surface, we found a total of 17 different arthropod taxa (Tab. S2, Appendix A), with the number of taxa ranging monthly from two (February, September–November; per trap location) to 13 taxa (April) (mean ± 1SE: 6.0 ± 0.1, $N = 210$) (Tab. S3a, b, Appendix A). In the unsaturated sediments, we found a total of 21 taxa (Tab. S2, Appendix A), ranging from one taxon (February–March, September–November) to nine taxa (June, July) (mean ± 1SE: 4.5 ± 0.1, $N = 330$) (Tab. S3c–l, Appendix A).

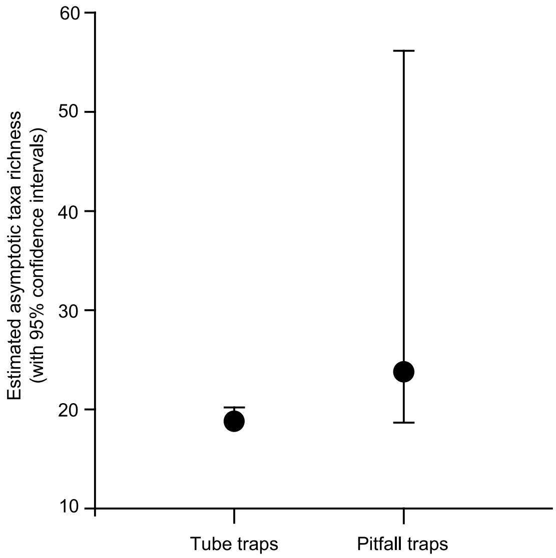


**Fig. 4.** Estimated total taxa richness on the sediment surface and within the unsaturated sediments, based on the two sampling methods.

Computing the mean Chao1 estimator revealed similar total taxa richness for aggregated subsurface samples (19; $N = 330$) and aggregated surface samples (24; $N = 210$) (Fig. 4). The large 95% CI of pitfall traps (18.9–56.4) was attributable to three taxa (Ephemeroptera, Opiliones, Hirudinea) being represented by only one individual each (Ellison et al., 2007).

Arthropod richness varied significantly with depth ($F_{3,154.6} = 19.5, P < 0.001$), lateral distance across the gravel bar ($F_{3,152.5} = 10.2, P < 0.001$), and over time ($F_{9,314.8} = 22.6, P < 0.001$). Significantly more taxa were found at the sediment surface than within the sediments, and significantly more taxa were found at the channel edge (1 m distance) than at locations towards the centre of the gravel bar (Fig. 3(c)). Within the sediment, we found a similar number of taxa at all three depths (Fig. 3(c)).

### 3.3. *Taxa composition*

The most abundant taxa found throughout the study, in decreasing order of abundance (pooled data), were: Coleoptera (30% of total abundance), Collembola (23.1%), Araneae (20.2%), Diptera (7.2%), Dermaptera (5.3 %), Acari (5.0%), Hymenoptera (4.4%), and Hemiptera (1.9%) (Fig. 5(a),(b)). Coleoptera were numerically the most abundant taxon on the sediment surface, whereas Collembola were the most abundant taxon within the sediment (Fig. 5(a)). Araneae were more likely to be captured on the surface than in the subsurface sediments. Dermaptera stayed almost exclusively on the sediment surface, and Cyclopoida, Lepidoptera larvae, Oligochaeta and Pseudoscorpiones were only caught, albeit in small numbers, within the sediment (Tab. S2, Appendix A). Concerning the lateral distribution of abundance, Coleoptera were numerically the most abundant at locations along the channels, Collembola in 5 and 20 m distance from the channel edges, and Acari in the centre of the gravel bar (60–100 m; Fig. 4(b)).

## 4. Discussion

We have shown that exposed riverine sediments are three-dimensional habitats that consist of the sediment surface and the unsaturated interstitial sediments lying beneath the surface and above the groundwater table. This so far neglected but extensive habitat hosts a diverse and abundant arthropod fauna. Although abundance and taxa richness were significantly lower within the sediment than at the surface, arthropods used the entire unsaturated zone that we studied as a habitat, with significant lateral gradients in density and taxa richness. Due to a considerable abundance at a depth of 1.1 m, we argue that riparian arthropods might use even deeper sediment layers, possibly down to the sediment–groundwater interface.

The relative importance of the unsaturated sediments for arthropods could even be higher than presently estimated. Due to the lower permeability of this zone compared to the sediment surface, we likely underestimated arthropod activity density in the subsurface sediments compared to catches at the surface. The difference in permeability may also have introduced a bias in tube trap samples towards smaller-bodied arthropods, similarly to the filtering effect in hyporheic samples (Boulton et al., 2004). Indeed, the most abundant taxa on the sediment surface were Coleoptera, whereas within the sediments Collembola outnumbered all others (Fig. 5). Further research should clarify the issues raised above as well as the optimal exposure duration for tube traps.

We have demonstrated that increased arthropod abundance and richness close to channel edges (compared to abundances towards the centre of the floodplain; Fig. 3), previously reported only for the sediment surface (Bates et al., 2007;

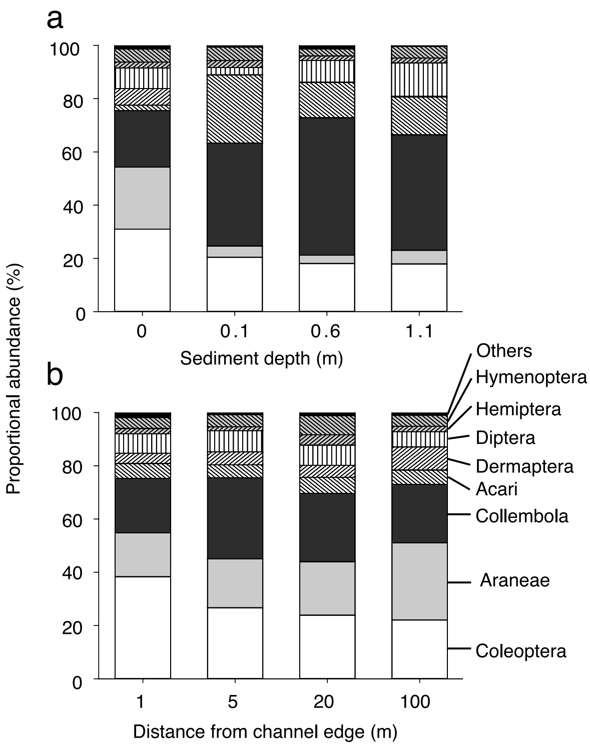


**Fig. 5.** Changes in arthropod composition (proportional abundance of eight different taxa) at four different depths (0, 0.1, 0.6 and 1.1 m; $N = 30$–210; (a), and four different distances from the channel edges (1, 5, 20, and 60–100 m; $N = 60$–90; (b). Others = arthropod groups that contributed $\leq 1\%$ to the total abundance.

Hering and Plachter, 1997; Paetzold et al., 2005), are transferable to the subsurface sediments. It suggests that connectivity between channels and gravel habitats in riverine floodplains, for example through the flow of nutrients and organic matter (Burdon and Harding, 2008), is not limited to the sediment surface and therefore more complex than assumed.

Spatial patterns in the abundance and richness of different taxa across the gravel bar were similar at the surface and in the subsurface sediments (Figs. 3 and 4) with a few taxa being almost exclusively caught in one or the other habitat (Fig. 5). This demonstrates that the arthropod fauna in the unsaturated sediments comprised taxa that are permanent residents of this habitat, as well as a large proportion of taxa that are usually found at the sediment surface but can exploit both habitats. Hence for these 'surface' taxa, the unsaturated sediments may represent a regularly used partial habitat as well as a temporary refugium. It may also well be that some species of these 'surface' taxa are permanent residents of the unsaturated zone or the sediment surface, respectively, and do not cross over between the surface and the subsurface sediment layers. Such a conclusion may be supported in the future employing a finer taxonomic level than in the present study.

Based on these findings, we speculate that the role of the unsaturated sediments (see below) may be similar to the saturated hyporheic and parafluvial zones. These zone can provide habitat for (aquatic) invertebrates down to at least 30 cm depth below the stream bed (Boulton et al., 1991; Marchant, 1988, 1995) and far out into the floodplain alluvium (Marmonier et al., 1992; Stanford and Ward, 1988), therewith connecting surface and groundwater vertically and horizontally. They substantially contribute to surface biodiversity and resilience through their multiple functions as a nursery, storage, and refuge zone, respectively (Dole-Olivier, 2011; Dole-Olivier et al., 2014).

Compared to the sediment surface, arthropod numbers remained relatively stable in the subsurface sediments throughout the study period, confirming that the unsaturated sediments are regularly used as a partial habitat by many taxa. Individual taxa exhibited different patterns in daily activity depending on their preferred temperature and humidity preferences. For example, many beetle species living on the surface of exposed riverine sediments are diurnal and therefore, most active when it is warm (Thiele, 1977). For these species, the unsaturated sediments probably represent an important partial habitat providing warmer temperatures at night-time and during cool weather conditions compared to the surface (Tonolla et al., 2010, Tab. S1b). Other groups, such as Collembola that are less tolerant of high temperature and low humidity conditions (Hopkin, 1997), presumably use the unsaturated sediments as a partial habitat during the day-time and during warm weather conditions. Future experiments including time-sorted pitfall- and tube-trapping coupled with telemetry (Kissling et al., 2014) are required to study short- and long-term dispersal and migration patterns.

To escape unfavourable but relatively predictable seasonal variations in temperature and soil moisture, such as the very low (in winter) or the very high temperatures (summer) on the sediment surface, arthropods may use the unsaturated sediments as a temporary refugium. While it is a common strategy of arthropods in temperate climates to avoid low winter temperatures in the resistant egg stage (Rothenbucher and Schaefer, 2006), spiders and carabid beetles associated with exposed sediments mostly overwinter as adults and occasionally as larvae (Andersen, 1968; Rothenbucher and Schaefer, 2006). Along the lower Oder River in Germany, for instance, 63% of spiders and 73% of carabid beetles overwintered in sheltered, vegetated areas, and migrated onto exposed river sediments in spring (Rothenbucher and Schaefer, 2006). However, although the whereabouts of the remaining assemblage is unknown, our data suggest that they could survive low winter temperatures closer to the river channel, in particular within the sediments. A similar strategy has been adopted by wetland carabid beetles in southern Sweden, which were found in winter quarters within 50 m distance from lakes and fens (Andersen, 2011). This may be true for other taxa and/or geographical regions as well. Although many arthropods rely on warm temperatures to be active, extreme heat can be lethal to them. For example, gravel specialists of the genus *Bembidion* (Coleoptera: Carabidae) do not survive temperatures above 37–42 °C (Andersen, 1986). However, temperatures in this range regularly occur on the surface of exposed sediments (Bates et al., 2009; Tonolla et al., 2010). Thus, such extreme temperatures may trigger less tolerant arthropods to shelter temporarily in the subsurface sediments.

Arthropods might also use the unsaturated sediments as temporary refugium to cope with the submersion of sediment surfaces due to seasonal variations in flow or stochastic flow and flood pulses. While adaptations to seasonal inundation are well studied for arthropods inhabiting Central Amazonian floodplains (Adis and Junk, 2002), surprisingly little is known about survival strategies of European arthropods. One of the few in-situ studies found that most plant- and leafhoppers along the Oder River in Germany overwintered in the floodplain, tolerating seasonal submersion (Rothenbucher and Schaefer, 2006). The study of Kolesnikov et al. (2012) also demonstrates that beetles can survive submersion up to two weeks under aerated conditions. Such conditions are comparable to the conditions within the sediments during surface inundation, when interstitial pores partially filled with air persist.

To our knowledge, this is the first study demonstrating that the extensive volume of unsaturated sediments along braided, gravel-bed rivers is an important habitat for a wide range of arthropods, most likely for various reasons. We are convinced that this study stimulates further research in different areas: Addressing the vertical and horizontal distribution and movement of arthropods within the unsaturated sediments, for example, will help to better understand the connection between the surface of exposed sediments and the groundwater or the hyporheic zone, respectively. Thereby, when considering expansion and contraction cycles, we will learn how these dynamics shape the unsaturated sediment-habitat and affect the behaviour of the arthropods living therein. Such studies may also explain the occurrence of strictly aquatic taxa such as Trichoptera larvae or Cyclopoida, which we have collected (in very low numbers) in the unsaturated sediments. Finally, studying the connection between the thermal regime and arthropod activity within and on the sediment surface will disentangle whether temperature effects occur at the daily, the seasonal and/or the taxa level.

## 5. Implications for conservation and management

Due to previous ignorance, anthropogenic threats to the unsaturated sediments, although manifold, have hardly been considered when managing gravel-bed rivers. Specifically, clogging of interstitial spaces with fine sediments reduces the habitat suitability for many species (Paetzold et al., 2008) and may prevent arthropods accessing deeper sediment layers. Clogging can be caused by an increase in the proportion of fine sediments due to flow regulation, within-channel gravel mining (Rinaldi et al., 2005), and/or by the winter die-back of invasive plant species that can increase the rate of bank-side fine sediment erosion during winter (Dawson and Holland, 1999). Livestock trampling also causes sediment compaction, which limits the availability of interstitial spaces (Bates et al., 2009). Hence we urge to include the unsaturated, interstitial sediments of gravel-bed rivers in science, conservation, and management programmes to help ensure the future of this dynamic and diverse habitat, and the functions it provides. Here, we provide the basis for future studies of this unexplored habitat which, if based on a fine taxonomic level, could potentially yield to new species some of which may be identified as threatened.

## Acknowledgements

We thank C. Cruciat and J. Rueegg for assistance in the field and Y. Lehnhard for providing Fig. 1. A. Bates, F. Altermatt, and five anonymous reviewers (two from this journal and three from Freshwater Biology) significantly improved an earlier version of this manuscript. The Eawag workshop team constructed the tube traps, and the Swiss Federal Institute for Forest, Snow and Landscape Research WSL (Switzerland) provided pitfall traps. This research was funded by the European Commission, and supported through the tempQsim-project (Contract No. EVK1-CT-2002-0012) and by the Swiss State Secretariat for Education and Research (SBF No. 02.0072). Simone Langhans was partly supported through the Alexander von Humboldt-Foundation.

## Appendix A. Supplementary data

Supplementary material related to this article can be found online at http://dx.doi.org/10.1016/j.gecco.2014.08.009.

## References

Adis, J., Junk, W.J., 2002. Terrestrial invertebrates inhabiting lowland river floodplains of Central Amazonia and Central Europe: a review. Freshwater Biol. 47, 711–731.
Andersen, J., 1968. The effect of inundation and choice of hibernation sites of Coleoptera living on river banks. Norsk Entomol. Tidssk. 15, 115–133.
Andersen, J., 1986. Temperature response and heat tolerance of riparian Bembidiini species (Coleoptera, Carabidae). Entomol. Gener. 12, 57–70.
Andersen, J., 2011. Winter quarters of wetland ground beetles (Coleoptera, Carabidae) in South Scandinavia. J. Insect Conserv. 15, 799–810.
Andersen, J., Hansson, O., 2005. Riparian beetles, a unique, but vulnerable element in the fauna of Fennoscandia. Biodiv. Conserv. 14, 3497–3524.
Baars, M.A., 1979. Catches in pitfall traps in relation to mean densities of carabid beetles. Oecologia 41, 25–46.
Bates, A.J., Sadler, J.P., Henshall, S.E., Hannah, D.M., 2009. Ecology and conservation of arthropods of exposed riverine sediments (ERS). Terres. Arthrop. Rev. 2, 77–98.
Bates, A.J., Sadler, J.P., Perry, J.N., Fowles, A.P., 2007. The microspatial distribution of beetles (Coleoptera) on exposed riverine sediments (ERS). Eur. J. Entomol. 104, 479–487.
Beattie, A.J., Oliver, I., 1994. Taxonomic minimalism. Trends. Ecol. Evolut. 9, 488–490.
Boulton, A.J., Dole-Olivier, M.J., Marmonier, P., 2004. Effects of sample volume and taxonomic resolution on assessment of hyporheic assemblage composition sampled using a Bou–Rouch pump. Archiv Hydrobiol. 159, 327–355.
Boulton, A.J., Stibbe, S.E., Grimm, N.B., Fisher, S.G., 1991. Invertebrate recolonization of small patches of defaunated hyporheic sediments in a Sonoran Desert stream. Freshwater Biol. 26, 267–277.
Burdon, F.J., Harding, J.S., 2008. The linkage between riparian predators and aquatic insects across a stream-resource spectrum. Freshwater Biol. 53, 330–346.
Caruso, B.S., 2006. Project river recovery: restoration of braided gravel-bed river habitat in New Zealand's high country. Environ. Manag. 37, 840–861.
Colwell, R.K., 2013. EstimateS: Statistical estimation of species richness and shared species from samples. Version 9. User's Guide and application published at: http://purl.oclc.org/estimates.
Colwell, R.K., Chao, A., Gotelli, N.J., Lin, S.-Y., Mao, C.X., Chazdon, R.L., Longino, J.T., 2012. Models and estimators linking individual-based and sample-based rarefaction, extrapolation, and comparison of assemblages. J. Plant Ecol. 5, 3–21.
Corti, R., Larned, S.T., Datry, T., 2013. A comparison of pitfall-trap and quadrat methods for sampling ground-dwelling invertebrates in dry riverbeds. Hydrobiologia 717, 13–26.
Datry, T., Corti, R., Belletti, B., Piégay, H., 2014. Ground-dwelling arthropod communities across braided river landscape mosaics: a Mediterranean perspective. Freshwater Biol. 59, 1308–1322.
Dawson, F.H., Holland, D., 1999. The distribution in bankside habitats of three alien invasive plants in the UK in relation to the development of control strategies. Hydrobiologia 415, 193–201.
Dieterich, M., 1996. Methods and preliminary results from a study on the habitat functions of the gravel bar interior in alluvial floodplains. Verhandl. Gesellsch. Ökol. 26, 363–367.
Doering, M., Uehlinger, U., Rotach, A., Schlaepfer, D.R., Tockner, K., 2007. Ecosystem expansion and contraction dynamics along a large Alpine alluvial corridor (Tagliamento River, Northeast Italy). Earth Surf. Process. Landf. 32, 1693–1704.
Dole-Olivier, M.-J., 2011. The hyporheic refuge hypothesis reconsidered: a review of hydrological aspects. Mar. Freshwater Res. 62, 1281–1302.
Dole-Olivier, M.-J., Maazouzi, C., Cellot, B., Fiers, F., Galassi, D.M.P., Claret, C., Martin, D., Mérigoux, S., Marmonier, P., 2014. Assessing invertebrate assemblages in the subsurface zone of stream sediments (0–15 cm deep) using a hyporheic sampler. Water Resour. Res. 50, 453–465.
Ellison, A.M., Record, S., Arguello, A., Gotelli, N.J., 2007. Rapid inventory of the ant assemblage in a temperate hardwood forest: species composition and assessment of sampling methods. Environ. Entomol. 36, 766–775.
Gotelli, N.J., Colwell, R.K., 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecol. Lett. 4, 379–391.
Habersack, H., Piegay, H., 2008. River restoration in the Alps and their surroundings: past experience and future challenges. In: Habersack, H., Piegay, H., Rinaldi, M. (Eds.), Gravel-bed Rivers VI: From Process Understanding to River Restoration. Elsevier, Amsterdam, The Netherlands, pp. 703–737.
Hammond, P.M., 1998. Riparian and floodplain arthropod assemblages: their characteristics and rapid assessment. In: Bailey, R.G., Jose, P.V., Sherwood, B.R. (Eds.), United Kingdom Floodplains. Westbury, Otley, UK, pp. 238–282.
Hering, D., Plachter, H., 1997. Riparian ground beetles (Coeloptera, Carabidae) preying on aquatic invertebrates: a feeding strategy in alpine floodplains. Oecologia 111, 261–270.
Hopkin, S.P., 1997. Biology of the Springtails, Insecta: Collembola. Oxford University Press, New York.
Hyman, P.S., 1992. A Review of The Scarce and Threatened Coleoptera of Great Britain (updated by M.S. Parsons). Part 1. JNCC, Peterborough.
Hyman, P.S., 1994. A Review of The Scarce and Threatened Coleoptera of Great Britain (updated by M.S. Parsons). Part 2. JNCC, Peterborough.
Kahlen, M., 2003. Die Käfer der Ufer und Auen des Tagliamento (Erster Beitrag: Eigene Sammelergebnisse). Gortania 24, 147–202.
Kahlen, M., 2009. The beetle fauna of the Tagliamento River flood plains and alluvial forests (II contribution: from own and of others collections and literature data). Gortania 31, 65–136.
Kissling, W.D., Pattemore, D.E., Hagen, M., 2014. Challenges and prospects in the telemetry of insects. Biol. Rev. 89, 511–530.
Kolesnikov, F.N., Karamyan, A.N., Hoback, W.W., 2012. Survival of ground beetles (Coleoptera: Carabidae) submerged during floods: Field and laboratory studies. European J. Entomol. 109, 71–76.
Langhans, S.D., Tiegs, S.D., Gessner, M.O., Tockner, K., 2008. Leaf-decomposition heterogeneity across a riverine floodplain mosaic. Aquatic Sci. 70, 337–346.
Longino, J.T., Coddington, J., Colwell, R.K., 2002. The ant fauna of a tropical rain forest: estimating species richness three different ways. Ecology 83, 689–702.
Luff, M.L., 1975. Some features influencing efficiency of pitfall traps. Oecologia 19, 345–357.
Marchant, R., 1988. Vertical distribution of benthic invertebrates in the bed of the Thomson River, Victoria. Aust. J. Marine Freshwater Res. 39, 775–784.
Marchant, R., 1995. Seasonal variation in the vertical distribution of hyporheic invertebrates in an Australian upland river. Archiv Hydrobiol. 134, 441–457.
Marmonier, P., Dole-Olivier, M.-J., Creuzé des Chatelliers, M., 1992. Spatial distribution of interstitial assemblages in the floodplain of the Rhône River. Regul. Rivers: Res. Manag. 7, 75–82.
Naiman, R.J., Decamps, H., Pollock, M., 1993. The role of riparian corridors in maintaining regional biodiversity. Ecol. Appl. 3, 209–212.
Paetzold, A., Schubert, C.J., Tockner, K., 2005. Aquatic terrestrial linkages along a braided-river: Riparian arthropods feeding on aquatic insects. Ecosystems 8, 748–759.
Paetzold, A., Yoshimura, C., Tockner, K., 2008. Riparian arthropod responses to flow regulation and river channelization. J. Appl. Ecol. 45, 894–903.
Petts, G.E., Gurnell, A.M., Gerrard, A.J., Hannah, D.M., Hansford, B., Morrissey, I., Edwards, P.J., Kollmann, J., Ward, J.V., Tockner, K., Smith, B.P.G., 2000. Longitudinal variations in exposed riverine sediments: a context for the ecology of the Fiume Tagliamento, Italy. Aquatic Conserv.-Marine Freshwater Ecosyst. 10, 249–266.
Rinaldi, M., Wyzga, B., Surian, N., 2005. Sediment mining in alluvial channels: physical effects and management perspectives. River Res. Appl. 21, 805–828.
Rothenbucher, J., Schaefer, M., 2006. Submersion tolerance in floodplain arthropod communities. Basic Appl. Ecol. 7, 398–408.
Sadler, J.P., Bell, D., Fowles, A., 2004. The hydroecological controls and conservation value of beetles on exposed riverine sediments in England and Wales. Biol. Cons. 118, 41–56.
Spence, J.R., Niemela, J.K., 1994. Sampling carabid assemblages with pitfall traps — the madness and the method. Can. Entomol. 126, 881–894.
Stanford, J.A., Ward, J.V., 1988. The hyporheic habitat of river ecosystems. Nature 335, 64–66.
Thiele, H.U., 1977. Carabid Beetles in Their Environments. Springer Verlag, Berlin Heidelberg.
Tockner, K., Stanford, J.A., 2002. Riverine flood plains: present state and future trends. Environ. Conserv. 29, 308–330.
Tockner, K., Ward, J.V., Arscott, D.B., Edwards, P.J., Kollmann, J., Gurnell, A.M., Petts, G.E., Maiolini, B., 2003. The Tagliamento River: a model ecosystem of European importance. Aquatic Sci. 65, 239–253.
Tonolla, D., Acuna, V., Uehlinger, U., Frank, T., Tockner, K., 2010. Thermal heterogeneity in river floodplains. Ecosystems 13, 727–740.
Ward, J.V., 1998. Riverine landscapes: Biodiversity patterns, disturbance regimes, and aquatic conservation. Biol. Conserv. 83, 269–278.