Soil invertebrate abundance, diversity, and community composition across steep high elevation snowmelt gradients in the European Alps

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ABSTRACT
We studied abundance, diversity, and composition of soil invertebrates along snowmelt gradients to generally understand how soil animal communities are responding to life conditions across snowbeds along a west–east transect of the European Alps and to create a reference inventory for future investigations of climate change effects on snowbed habitats. We extracted microarthropods (collembolans, oribatid mites) and macroinvertebrates (spiders, beetles, insect larvae) from soil cores taken from three sections along the snowmelt gradient: high (early snowmelt), middle, and low (late snowmelt) sections. Linear models showed no correlations between either soil conditions or time of snowmelt and densities of soil animals. A small, though statistically significant, variation in the generally high soil organic matter and sand contents and high porosity of snowbed soils seems to have no effect on soil invertebrates. Species found along the snowmelt gradient were in similar shares generalist and specialist species. Microarthropod community composition in general was driven by soil porosity and soil organic matter content; for macroinvertebrate community composition we found no specific driver. We conclude that invertebrate species assemblages in snowbeds are rather similar in the European Alps.

Introduction
Snowbeds are depressions where snow accumulates and does not melt until late in the growing season, resulting in characteristic plant communities dominated by bryophytes, small perennial hemicyryptophytes, and prostrate dwarf shrubs at the base of the snowbed, flowing into graminoid-dominated alpine grassland vegetation at the upper edge. Steep snowmelt gradients across snowbeds are commonly found above the alpine treeline and represent “experiments by nature” that permit testing hypotheses related to the effect of snowpack duration (season length) over very short spatial distances. Snowbeds are characterized by short growing seasons (Friedel 1961; Körner 2003; Matteofo et al. 2016), gradients in nutrient contents (Little et al. 2016), and stable soil temperatures during the snow cover season (Shimono and Kudo 2003; Körner et al. 2019), resulting in rather stable microbial activities (Schimel, Bilbrough, and Welker 2004) and rates of litter decomposition (Carbognani, Petraglia, and Tomaselli 2014) throughout the cold months. Communities inhabiting snowbeds are an important component of alpine biodiversity because they consist of species specifically adapted or restricted to these habitats (Björk and Molau 2007), even comprising endemic species (Dullinger, Dirnböck, and Grabherr 2000), but mostly species with a broad ecological amplitude. Until now, most snowbed studies focused on plant species richness (Domènech et al. 2016; Gritsch, Dirnböck, and Dullinger 2016), plant phenology after release from snow (e.g., Galen and Stanton 1995; Huelber et al. 2006; Sedlacek et al. 2015; Carbognani et al. 2016), the biology of snowbed specialist plant species (Llvent et al. 2013; Petraglia et al. 2014; Körner et al. 2019), or the impact of snow(melt) on plant community composition (e.g., Fowler and Overby 2016; Tonin et al. 2019).

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1Deceased.
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However, even though the importance of the linkage between above- and belowground communities has been emphasized many times (e.g., de Deyn and van der Putten 2005; Kardol and Wardle 2010), the role of alpine soil invertebrates inhabiting snowbeds still awaits exploration, despite their being central for ecosystem functioning (Eisenhauer 2012; Römcke, Bernard, and Martin-Laurent 2018; Eisenhauer, Bonn, and Guerra 2019). Except for two very early studies on snowbed invertebrates in Norway (Havgjer, Melaen, and Ostbye 1974) and New Zealand (Dickinson et al. 1998) and two more recent studies from the Snowy Mountains of Australia (Green and Slattery 2019) and from alpine habitats in New Zealand (Minor, Babenko, and Ermilov 2017), we found no other study on soil invertebrates permanently populating snowbeds. More local studies investigated community succession along glacier melt gradients rather than in snowbeds (Janetschek 1993; Kaufmann 2001) or community composition in alpine habitats in general (Haybach 1992; Steinwandter et al. 2018; Winkler et al. 2018).

As the climate will continue to warm in the European Alps at the current higher than average rate (Beniston et al. 2003; Beniston 2006; Hock et al. 2019), snowmelt regimes will change and so will the life conditions across snowmelt gradients (Vorkauf et al. 2021). Due to their very nature (i.e., their dependence on snow), snowbed communities are potentially more affected by climatic warming than other alpine biota. Changes in snowpack duration affect plant growth via time availability for resource assimilation (Galen and Stanton 1995), which may in turn affect resource availability for invertebrate species. Also, shorter periods of snow cover may change the microclimate (Matteodo et al. 2016) and impact life cycles (Søvik et al. 2003). Some of these changes may already be under way (Carbognani, Petraglia, and Tomaselli 2012; Gritsch, Dirnböck, and Dullinger 2016; Matteodo et al. 2016), causing plant productivity and the amount and quality of litter input and seasonal decomposition to change (Carbognani, Petraglia, and Tomaselli 2014), which may incur changes of functional species richness or even the local loss of specialist species (Komac et al. 2015). Here, we present one of very few studies on soil invertebrate abundances and diversity, their community composition, and their distribution along snowmelt gradients in the European Alps. We expect the snowmelt gradients across the snowbeds to represent a short distance gradient otherwise laid out for several hundred meters, with early snowmelt on the upper edge and late snowmelt at the bottom of the snowbed. The purpose of the study is, first, to generally understand which soil invertebrates are adapted to life conditions across snowbeds and, second, to create a reference inventory for future investigations of climate change effects on snowbed habitats. We hypothesize that invertebrate species composition will change along the snowmelt gradient due to the concomitant change in vegetation, as snowbeds host plant communities with a close to maximum productivity at the edge and a regional minimum productivity at the bottom of the snowbeds. For plants it has already been shown that snowbed communities comprise many specialist species, which will very likely also hold true for soil invertebrates. We therefore hypothesize that the soil community will comprise a high proportion (up to 50 percent) of specialist species that are adapted to snowbed conditions (e.g., hygrophilous, muscicicolous, or lichenicolous species). Monitoring especially these specialists will help us in future to predict effects of climatic warming, because they will very likely be the first species to be affected by changing snowmelt regimes.

### Material and methods

#### Study areas

The study was conducted as part of the Long-term Monitoring of Ecosystem Processes Programme of the Austrian National Park Hohe Tauern (Körner et al. 2019) and comprised three sites within the National Park (Innerschloss [IN], Untersulzbachtal [UN], Seebachtal [SE]), as well as two LTER/LTSER (Long-term (Socio-)Ecological Research) sites (LTER-Switzerland, Alpine Research Station Furka, ALPFOR, Switzerland [FU]; LTER IT25, Val Mzia/ Matschertal, Italy [OB]; Figure S1a). In total, twenty-two transects (each 3 m wide, 7–10 m long) representing snowmelt gradients were established at elevations between 2,300 and 2,700 m.a.s.l.; that is, 200 to 450 m above the local climatic treeline (for details on the

| Site         | Country/region       | Latitude (° N) | Longitude (° E) | Elevation (m.a.s.l.) | Exposition | Sampling date | Number of transects |
|--------------|----------------------|----------------|-----------------|----------------------|------------|---------------|---------------------|
| Furka        | Switzerland, Uri, Furka pass | 46.57789       | 8.42011         | 2.467                | S          | 7 August 2017 | 5                   |
| Oberettes    | Italy, South Tyrol, Matsch Valley | 46.76646       | 10.71140        | 2.700                | N and ESE  | 18 July 2017  | 3                   |
| Untersulzbachtal | Austria, Salzburg, Untersulzbachtal Valley | 47.16612       | 12.33073        | 2.380                | W          | 17 August 2017 | 6                   |
| Innerschloss | Austria, Tirol, Innerschloss | 47.11110       | 12.42656        | 2.350                | SW         | 16 August 2017 | 5                   |
| Seebachtal   | Austria, Kärnten, Mallnitz | 47.03899       | 13.18273        | 2.303                | N and S    | 15 August 2017 | 3                   |
individual sites see Table 1). Each transect was divided into three subtransects named A, B, and C, with the central B transect spared for nondestructive observations (Figure S1b). Vertically, each subtransect was separated in 1-m quadrats. The highest two to three quadrats (H, shortest snow duration) represent local close to maximum plant productivity, and the plant community is a typical alpine grassland dominated by graminoids such as Carex curvula. The middle part (M) is the transition zone, and the lowest two to three quadrats (L, longest snow duration) represent lowest plant productivity, with plant communities comprising bryophytes, small perennial herbs (e.g., Soldanella pusilla), and prostrate dwarf shrubs (e.g., Salix herbacea).

**Soil invertebrates—Microarthropods**

We used vertically stratified samples to evaluate the abundance and diversity of soil microarthropods (collembolans, oribatid mites). First, a 10 × 10 cm frame was fixed to the ground in either the A or C subtransect to vacuum the 100 cm² area for all epigean animals using a small customized, battery-driven hand vacuum cleaner (Figure S2). Next, the vegetation was cut at soil surface (the material was used for a different research module), followed by coring the center of the harvested area using an O’Connor splitcore soil sampler containing PVC tubes (Figure S1; inner diameter 4.8 cm, each tube 5 cm high). Depending on the profile depth (e.g., stones), the soil core was divided into two or three layers (0–5 cm, 5–10 cm, and 10–15 cm, if available), including the litter and raw humus layer in the top core. Each core was closed with lids at the top and bottom, and samples were transported to the soil laboratory at the University of Innsbruck in a cool box within less than three days. For each of the five sites, thirty sample locations were selected (ten for each transect section H, M, and L), evenly distributed among the available number of transects. This resulted in a total of 507 mesofauna samples (i.e., 5 sites × 30 sample locations × available number of strata).

Soil microarthropods were extracted by heat with a Macfadyen High Gradient apparatus for eight to ten days (Macfadyen 1953); the collection fluid was saturated saltwater. After extraction, all animals were transferred into a sieve (mesh size 500 μm) and rinsed in tap water, fixed in 75 percent ethanol, and identified to species level (adult specimens) using a stereomicroscope following the identification keys of Weigmann (2006) for oribatid mites and Bretfeld (1999), Fjellberg (1998, 2007), Potapov (2001), and Thibaud, Schulz, and Da Gama Assalino (2004) for collembolans. For more details on methods, see Meyer (2019).

Abundances of species per sample plot were extrapolated to individuals per square meter to account for different sample areas of litter (100 cm²) and soil samples (18.1 cm²). Because there were only very few soil invertebrates at soil depths below 5 cm, these few individuals were added to the 0–5 cm sample for further statistical analyses.

**Soil invertebrates—Macrofauna**

At three out of the five study sites (Furka, Oberettes, Innergschlöss) additional soil samples were taken as larger soil blocks to obtain soil macroinvertebrates (invertebrates > 2 mm; e.g., spiders, beetles, insect larvae). Due to the destructiveness of sampling such soil blocks, these were taken from outside the transects at the three sites (but close to and vertically aligned to the H, M, L sections).

At each of the three sites, eighteen samples (20 × 20 cm, 10–15 cm deep depending on soil depth) were taken from three selected snowbeds (six samples in each transect section H, M, and L), put into linen bags, and transported to the soil lab. From these fifty-four macrofauna samples, soil animals were heat-extracted for twelve days using a modified Kempson apparatus (Kempson, Lloyd, and Ghelardi 1963), with propylene glycol as collection fluid. After extraction, soil animals were transferred to 75 percent ethanol and identified using a dissection stereomicroscope. Taxonomic identification followed Schaefer (2009). The physical and chemical soil characteristics of these soil blocks were assumed to match those obtained nearby by soil cores. As with mesofauna species, abundances were extrapolated to individuals per square meter.

**Soil parameters**

At each site two types of soil samples were taken for physical and chemical analysis and root sampling: undisturbed cylinder samples and disturbed dug-out samples of similar volume. The cylinder samples are required for the analysis of the soil water balance (pF curve) and for the determination of the root biomass. The disturbed samples were needed for the analysis of soil texture and soil chemical parameters. The samples were taken from the top 6 cm (excluding the litter and top raw humus layer). The cylinders had a volume of 100 cm³ (diameter of 5 cm and a height of 5 m), and the disturbed sample had at least 150 g dry weight. Cylinder samples were completely saturated in a water bath before further analyses; the disturbed soil samples were air-dried and then sieved to 2 mm. Altogether, 116 soil samples were taken (FU: 29, OB: 15, UN: 30, IN: 25, SE: 17).
To obtain soil organic matter content (SOM), 5 g of air-dried soil was incinerated at 550°C for 3 hours in a muffle furnace (all sites had silicate bed rock; hence, there was no need for a carbonate treatment). The pH curve was measured using an automated analyzing system (HYPROP, Meter Group, Munich, Germany) following the manufacturer’s guidelines. Soil texture was assessed by means of an automated measuring device (PARIO, Meter Group) following the manufacturer’s guidelines with slight modifications in the sample preparation, because the content of hardly decomposable organic matter in the samples was very high. Therefore, the time for the destruction of the organic matter was extended and the addition of H₂O₂ increased. Soil chemical analyses were carried out at the Research Center Laimburg (Bozen/Bolzano, Italy) following standard protocols (Table S1). For more details on methods, see Newesely, Tappeiner, and Körner (2019).

**Root mass**

For the determination of the belowground plant biomass (root biomass), sample cylinders were taken in addition to the soil samples at the same plots and soil depths. The roots were washed out in the laboratory under running water in three rinsing cycles (with sieves of 2 mm, 1 mm, and 0.5 mm mesh width, respectively) and then dried at 80°C and weighted. For more details on methods, see Newesely, Tappeiner, and Körner (2019).

**Data on snow cover**

In each section (H, M, L) of each transect a soil temperature logger was installed at 3- to 4-cm depth in subtransect B (iButton DS 1922L, with measuring interval of 3 hours). The time point of snowmelt can be clearly identified by the sudden temperature jump from near 0°C to positive temperatures. The opposite pattern applies to the time point of snowing in early autumn. Loggers have been continuously measuring soil temperature since the beginning of the project, and we used data from four years (2017–2020) to evaluate mean snowmelt patterns for each site (Table 2).

**Statistical analyses**

Differences in soil parameters, in total abundances (individuals per square meter per sampling plot) of microarthropods and macroinvertebrates, and in species richness (number of species per sampling plot) between sites were analyzed by linear models (LMs) with site as factor, followed by Tukey’s post hoc tests at a significance level of \( p < .05 \) using the R package `multcomp` (Hothorn et al. 2019). Differences in abundances between generalist and specialist species for each site were also analyzed by LMs with factors ecological type (generalist/specialist) and site. To analyze differences in soil parameters and snow cover (day of year of snowmelt, duration of snow cover) between transect sections (H, M, L), we used linear mixed effect models (LMEs) with site as a random effect to account for site-specific differences using R package `lme4` (Bates et al. 2015). The same procedure was used to test for the effect of day of year of snowmelt and duration of snow cover on abundances of invertebrates. Generalized linear models with a Gamma distribution (due to positively skewed abundance data) were used to test for correlations between soil parameters and abundances of invertebrates. Before doing so, we calculated intracorrelation coefficients to test whether adding site as random effect is necessary here as well; however, intracorrelation coefficients revealed no dependencies. For each model, specifications and residual diagnostics were performed with R package `DHARMa` (Hartig 2020) and model quality and goodness-of-fit were evaluated with R package `performance` (Lüdecke, Makowski, and Waggner 2020).

For each site we calculated both the Shannon–Weaver diversity and Simpson diversity using R package `vegan` (Oksanen et al. 2019), and to test for differences in species diversity among sites, we employed LMs.

Community compositions of microarthropods and macroinvertebrates were analyzed via nonmetric multidimensional scaling (NMDS) using Bray-Curtis distance with function `metaMDS` in R package `vegan`. To test for significant differences in community composition between sites and transect sections, we employed permutational multivariate analyses of variance.
(PERMANOVAs) with function adonis in R package vegan. To evaluate the effect of soil parameters on community composition, we calculated constrained analyses of principal coordinates using Bray-Curtis distance with functioncapscalein R package vegan. To obtain the best-fitting model, a combination of an a priori selection of predictors based on expertise and a forward selection approach was employed. We first selected soil parameters with low correlation coefficients to other parameters to avoid multicollinearity but chose at least one parameter out of the following groups: soil texture (amount of sand, silt, and clay), soil nutrients (soil organic matter content, total nitrogen, cation exchange capacity, saturation), and soil physical parameters (porosity, bulk density, pH values). Starting from the full model, we then continuously dropped nonsignificant terms until only significant ones were left. All analyses were computed using R (v4.0.2; R Core Team 2020) in R Studio (v1.3.959; R Studio Team 2020).

## Results

### Soil properties

Except for root mass and clay content, soil parameters differed significantly among sites (Table 3), even though within-site variation was mostly rather high. Noteworthy is the high variation in SOM and total nitrogen (N_{total}) in the Seebachtal transects. Significant differences along the snowmelt gradient were found only for porosity and bulk density. Soil porosity increased significantly from L to H (LME, Tukey contrasts: p = .005), whereas bulk density significantly decreased (LME, Tukey contrasts: p = .006).

### Snow cover

We evaluated data on snow cover (day of year of end of snowmelt, duration of snow cover) for the year 2017 (sampling year of soil fauna) as well as for all four years

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**Table 3. Descriptive means (SDs) of soil parameters for each site and section.**

|                  | Furka      | Obereutes | Untersulzbach | Innereglirsch | Seebachtal | p Value |
|------------------|------------|-----------|---------------|---------------|------------|---------|
| **Root mass (g)**|            |           |               |               |            |         |
| H                | 1,269.6    | 1,120.5   | 950.7         | 856.8         | 1,002.2    | 0.496   |
| M                | 906.6      | 1,049.4   | 745.2         | 666.6         | 1,175.4    | 0.247   |
| L                | 1,373.1    | 1,039.6   | 744.7         | 583.9         | 912.8      | 0.673   |
| Mean             | 1,165.8    | 1,040.3   | 809.3         | 698.2         | 1,016.9    | 0.467   |
| **Porosity (vol%)**|           |           |               |               |            |         |
| H                | 0.686      | 0.308     | 0.317         | 0.970         | 0.823     | 0.057   |
| M                | 0.670      | 0.320     | 0.688         | 0.843         | 0.840     | 0.080   |
| L                | 0.628      | 0.620     | 0.712         | 0.656         | 0.860     | 0.108   |
| Mean             | 0.659      | 0.620     | 0.806         | 0.718         | 0.840     | 0.073   |
| **Bulk density (g/cm³)**|      |           |               |               |            | <.001   |
| H                | 0.832      | 0.108     | 0.910         | 0.492         | 0.473     | 0.149   |
| M                | 0.868      | 0.150     | 0.415         | 0.827         | 0.413     | 0.215   |
| L                | 0.985      | 0.101     | 0.706         | 0.906         | 0.367     | 0.300   |
| Mean             | 0.903      | 0.101     | 0.518         | 0.747         | 0.423     | 0.200   |
| **SOM (%)**      |            |           |               |               |            | <.001   |
| H                | 10.3       | 18.7      | 26.4          | 22.5          | 28.9      | 0.130   |
| M                | 6.1        | 24.4      | 24.4          | 17.5          | 39.5      | 0.247   |
| L                | 8.3        | 23.5      | 13.5          | 6.5           | 42.7      | 0.210   |
| Mean             | 8.4        | 22.2      | 22.7          | 15.5          | 36.2      | 0.182   |
| **N_{total} (%)**|            |           |               |               |            | <.001   |
| H                | 0.374      | 0.770     | 0.982         | 0.744         | 0.970     | 0.526   |
| M                | 0.243      | 1.007     | 0.960         | 0.628         | 0.163     | 0.699   |
| L                | 0.317      | 0.937     | 0.565         | 0.308         | 1.467     | 0.707   |
| Mean             | 0.316      | 0.904     | 0.862         | 0.560         | 1.177     | 0.599   |
| **Cation exchange capacity (mmol/kg)**|     |           |               |               |            | <.001   |
| H                | 69.0       | 90.7      | 109.4         | 88.8          | 93.3      | 0.196   |
| M                | 57.3       | 104.0     | 100.8         | 72.2          | 116.0     | 0.502   |
| L                | 69.5       | 100.7     | 75.7          | 36.8          | 120.0     | 0.344   |
| Mean             | 66.1       | 98.4      | 92.1          | 65.9          | 108.1     | 0.118   |
| **pH**           |            |           |               |               |            | <.001   |
| H                | 3.600      | 3.700     | 3.580         | 3.480         | 3.320     | 0.101   |
| M                | 3.988      | 3.700     | 3.570         | 3.520         | 3.330     | 0.231   |
| L                | 3.622      | 3.700     | 3.600         | 3.740         | 3.430     | 0.310   |
| Mean             | 3.717      | 3.700     | 3.580         | 3.580         | 3.360     | 0.013   |
| **Clay (%)**     |            |           |               |               |            |         |
| H                | 5.0        | 12.3      | 12.6          | 11.8          | 15.5      | 0.111   |
| M                | 8.0        | 9.7       | 15.7          | 14.1          | 4.3       | 3.9     |
| L                | 1.3        | 22.7      | 5.3           | 9.4           | 0.0       | 0.0     |
| Mean             | 4.4        | 14.9      | 11.9          | 11.9          | 7.5       | 0.7     |
| **Silt (%)**     |            |           |               |               |            |         |
| H                | 40.5       | 32.3      | 38.0          | 22.8          | 22.5      | 0.483   |
| M                | 42.0       | 41.3      | 37.0          | 21.7          | 34.0      | 0.817   |
| L                | 54.8       | 32.7      | 32.8          | 17.8          | 37.3      | 0.216   |
| Mean             | 45.4       | 35.4      | 36.2          | 20.7          | 30.4      | 0.007   |
| **Sand (%)**     |            |           |               |               |            | <.001   |
| H                | 54.8       | 55.7      | 49.6          | 65.5          | 61.8      | 0.751   |
| M                | 49.5       | 49.0      | 47.3          | 64.0          | 61.7      | 0.491   |
| L                | 44.3       | 44.3      | 62.0          | 73.2          | 62.7      | 0.216   |
| Mean             | 50.1       | 49.7      | 52.0          | 67.5          | 62.0      | 0.503   |

Note. Subscript letters indicate significant differences between sites (irrespective of subsections, results of tests for differences between sections within each site are indicated in the text).

Mean = overall mean for site.
for which data were available (2017–2020). Day of year of end of snowmelt and duration of snow cover differed significantly between sections L and H when considering data for 2017 only (LME, Tukey contrasts: \( p = .002 \) for day of year of end of snowmelt; LME, Tukey contrasts: \( p = .012 \) for duration of snow cover) as well as when including data from all four years (LME, Tukey contrasts: \( p = .001 \) for day of snowmelt; LME, Tukey contrasts: \( p = .002 \) for duration of snow cover). Estimated mean difference in end of snowmelt between sections L and H was eighteen days.

Snowmelt finished earliest in 2017 in the Seebachtal transects (Table 2) and latest at the Furka in section H (the highest point of the snowmelt gradient). The lowest point of the snowmelt gradient (section L) was covered with snow the longest in the Innerrglschlöss, which was derived from the latest mean day of year of end of snowmelt as well as from the longest mean duration of snow cover.

**Soil invertebrate abundance**

In total, we obtained 8,678 adult collembolans belonging to twenty-five species in ten families, 5,216 adult oribatid mites belonging to forty-nine species in twenty-four families, as well as 1,639 macroinvertebrates mostly belonging to spiders, beetles, and insect larvae (Tables S2, S3, S5).

The significantly highest mean abundance of collembolans was found at the Furka, followed by the Seebachtal, and the lowest mean abundance was obtained from Oberettes (LM: \( F_{4,142} = 6.51, p < .001; \) Figure 1a). No significant difference in Collembola abundance was found among transect sections L, M, and H along the snowmelt gradient, but the highest abundances were still recorded from the bottom of the gradient (section L). No correlation between the total abundance of collembolans and any soil parameters was detected. In addition, no effect of day of snowmelt or of duration of snow cover could be statistically detected.

Oribatid mites were most abundant in the Untersulzbachtal, followed by Oberettes, and the lowest abundance of mites was recorded from the Seebachtal (LM: \( F_{4,141} = 4.55, p = .002; \) Figure 1b). Again, no significant difference was found in mean oribatid mite abundance among transect sections, but in contrast to the collembolans, the highest abundance was found at the top of the snowmelt gradient (transect section H). Again, no effect of soil parameters, day of snowmelt, or duration of snow cover could be statistically detected.

Surprisingly, no significant differences were found for macroinvertebrate abundances, either among sites or among the H, M, L sections of the snow duration gradients along the transects. Again, we found no correlations between abundances of macroinvertebrates and any of the soil or snow parameters.

**Species/taxon richness and community composition**

Altogether, we found seventy-four soil microarthropod species; the most species-rich site was the Seebachtal (seventeen collembolan and twenty-five oribatid mite species), followed by the Furka (thirteen collembolan and twenty-two oribatid mite species), and the least species were found at Oberettes (ten collembolan and eighteen oribatid mite species; LM: \( F_{4,148} = 2.73, p = .031 \)). Eleven species (five collembolan and six oribatid mite species; that is, 15 percent of all microarthropod species) were found at all five sites, and the most common species (found at all sites with high abundances) was *Pseudosotoma sensibilis* Tullberg, 1876 (Collembola). On the other hand, thirty-six species (nine collembolan and twenty-seven oribatid mite species; that is, 49 percent of all species) were unique to one site, and most were recorded from the Seebachtal (five

![Figure 1](image-url). Mean abundances (individuals per square meter, in log scale) of (a) collembolans and (b) oribatid mites within each research site. Different letters above box plots indicate significant differences in abundances between sites. FU = Furka, OB = Oberettes, UN = Untersulzbachtal, IN = Innerrglschlöss, S = Seebachtal.
collembolan and eleven oribatid mite species). These unique species were mostly found in very low abundances, whereas the more common species (occurring in at least three sites) showed high abundances (Tables S2, S3). Shannon-Weaver diversity (Figure 2) and Simpson diversity differed significantly among sites (LM: $F_{4,148} = 4.21, p = .003$; LM: $F_{4,148} = 7.73, p < .001$, respectively), and the highest diversity was recorded for the Seebachtal transects (Shannon-Weaver 1.57, Simpson 0.72) and Oberettes (1.52, 0.78). Most species found along the snowmelt gradient were in similar shares generalist or specialist species (i.e., species adapted to conditions specifically associated with alpine snowbeds such as alpine, hygrophilous, lichenicolous, or muscicolous species; see Table S4). For oribatid mites the proportions of generalists and specialists were balanced; we found no significant differences in abundances of both ecological groups within each site. For collembolans we found a significantly higher number of specialists in snowbeds of the Seebachtal (Figure 3); in all other sites the proportions were again statistically balanced.

Furka also harbored the most macroinvertebrates (820 individuals), followed by the Innerschloss (445) and Oberettes (374). Most individuals were larvae of true flies (Brachycera, 164 individuals) or beetles (adults and larvae, 109 individuals; Table S3).

NMDS analysis of macroarthropods showed that community composition was quite similar at all five sites, with big overlaps between sites (Figure 4), except for Oberettes, which did not overlap with Innerschloss and Untersulzbachtal. Nevertheless, PERMANOVA revealed significant differences in community composition among sites (PERMANOVA: $p = .001$). The same is true for collembolans (not shown), oribatid mites (not shown), and macroinvertebrates (Figure 3b): we found large overlaps between sites but still significant differences in community composition ($p = .001$ for all three PERMANOVAs). We found no differences in species assemblages between transect sections H, M, and L.

Drivers of snowbed community composition

Constrained MDS revealed that microarthropod community composition in general was mainly driven by soil porosity ($p = .001$) and soil organic matter content ($p = .001$). The same parameters were responsible for community composition of collembolans ($p = .001$ and $p = .002$, respectively), whereas oribatid mite communities were driven by soil porosity ($p = .001$) and silt ($p = .011$). No parameters were found that significantly affected community composition of macroinvertebrates.

Discussion

Our analysis of diversity and abundance of soil invertebrates together with soil properties across steep snowmelt gradients at five alpine sites, widely spaced over the European Alps, revealed a surprisingly small variation in soil characteristics, associated with a similarly surprising small variation in invertebrate species distribution.

Figure 2. Shannon-Weaver index for microarthropod diversity within each research site. Different letters above boxplots indicate significant differences in microarthropod diversity between sites. FU = Furka, OB = Oberettes, UN = Untersulzbachtal, IN = Innerschloss, S = Seebachtal.
Contrary to our expectations, data on snowmelt patterns revealed only a small difference between high (early snowmelt) and low (late snowmelt) sections of less than three weeks.

All five study sites are located on silicate bedrock; therefore, pH values are low (all mean values are <4). The twenty-two snowbeds investigated in this study generally exhibit high organic matter contents; the Seebachtal transects with a mean SOM of 31 percent are particularly striking. Due to the high sand content and the high porosity, soils tend to warm up and dry out during the short snow-free period; thus, decomposer activity might be limited, thereby retarding litter decomposition (Carbognani, Petraglia, and Tomaselli 2012) and leading to an increase in organic matter content. Similar soil features (high organic matter content, high soil porosity, high sand content) have been reported for snowbeds in the Rhaetian Alps (Carbognani, Petraglia, and Tomaselli 2012) and the Upper Engadine (Hiller et al. 2005). Even though we found statistically significant differences in soil parameters among sites, contents of SOM and sand as well as soil porosity are already at
such a high level that it was not surprising that these soil characteristics did not significantly correlate with abundances of soil invertebrates.

Soil invertebrate communities were dominated by microarthropods (approximately 26,000 ind/m² on average per sample plot); far fewer macroinvertebrates were found (approximately 760 ind/m² on average per sample plot). Temperature is a major regulator of metabolic activity of soil invertebrates, and collembolans and oribatid mites are better adapted to low temperatures during the snow cover season and short vegetation periods than macroinvertebrates (Lavalle and Spain 2001; Teets and Denlinger 2014). Especially for earthworms, the low temperatures restrict their ability to inhabit snowbeds (Meshcheryakova and Berman 2014), and the poorly developed soils (all Leptosols) provide limited habitat for burrowing earthworms. We found mostly poorly mobile larvae of true flies as well as surface-active beetles (ground and rove beetles), which predate on microarthropods (König, Kaufmann, and Scheu 2011; Raso et al. 2014).

We found around 5,000 to 24,000 collembolans and 6,000 to 18,000 oribatid mites per square meter, but these numbers are much lower than those reported from snowbeds in Norway, where similar sampling methods have been used (Hagvar, Melaen, and Ostbye 1974), and also much lower compared to those of lowland habitats (Coleman, Callaham, and Crossley 2017), very likely owing to the particular soil and climatic conditions of snowbeds (e.g., the location in depressions and the resulting late snowmelt). We found no differences in abundance of microarthropods or species composition between bottom, middle, and top of the snowmelt gradient, very likely because the animals, in contrast to plants, are mobile and can move between these zones (Green and Slatyer 2019). Both collembolans and oribatid mites have been shown to inhabit the intranivean space, where they use the pores between snow crystals (Hågvar 2010) and can therefore move even during the season with snow cover. Other studies have shown that arthropod communities depend on snowmelt patterns and time of snowmelt (Leingärtner, Krauss, and Steffan-Dewenter 2014; Green and Slatyer 2019); however, contrary to our expectations, we could not verify this in our study, most likely due to the small difference in end of snowmelt between sections L and H. In general, collembolans are short-lived invertebrates, completing several generations per year, whereas oribatid mites have a life cycle of approximately two years. However, for both taxa studies in arctic and alpine regions have shown that they adapt to cold conditions by extending their life cycle to two years (collembolans) and even up to five years (oribatid mites; Søvik et al. 2003 and citations therein). In our opinion the small difference in the duration of snow cover between L and H along the snowmelt gradient does not bias abundances of these animals due to different longevity, because they already extended their life cycle over a longer period.

Species composition was similar shares (i.e., 50 percent each) made up of euryoecious species and species adapted to snowbed conditions. The species with the highest density by far, the collembolan Pseudosotoma sensibilis, a widespread palaeartic species living in the upper soil layer (Christian 1987), was found at all five sites. The most abundant oribatid mite that was found at all five sites, Tectocephus velatus (Michael, 1880), is an euryoecious cosmopolitan species (Schatz 1983). In contrast, species with special habitat requirements such as lichens, mosses, or high moisture contents (e.g., the collembolans Sminthurides schoetti Axelson, 1903 and Tetracanthella afurcata Handschin, 1919 or the oribatid mites Melanozetes meridianus Sellnick, 1928 and Oribatula interrupta [Willmann, 1939]) were found in highly variable densities. We even found two oribatid species endemic to the Alps, Kunstadamaeus diversipilis (at Furka and Untersulzbachtal with mean abundances of approximately 670 ind/m²) and Trichoribates scilierensis (at Furka, Oberettes, and Seebachtal with mean abundances of approximately 1,730 ind/m²). Species diversity was highest at the Seebachtal and Oberettes (Figure 2); the former harbored a range of species that were unique to this site but were found in very low densities (mostly just one individual in one sample). Due to some widespread species occurring in high densities in (almost) all sites, NMDS results exhibited large overlaps between sites, but species space was especially large for the Seebachtal (Figure S3a). Snowbeds of the Seebachtal differed from those of the other regions in that they offered little soil to sample and showed the least pronounced snowmelt gradients, and one of the three Seebachtal transects did not fully meet the requirements of a snowbed (being flatter, wind-exposed, and covered with dwarf shrubs). In addition to species diversity, species richness was highest in these transects. Aside from characteristic snowbed species such as T. afurcata and euryoecious species such as P. sensibilis, they harbored collembolan and mite species that are usually not found in snowbeds; for example, silviculous species (Caleremaeus montilipes (Michael, 1882), Conopippa palmicincta (Michael, 1884), Phthiracarus globosus) (Koch, 1841), Oribatida, probably brought there by grazing cattle. However, because these species were found in such low abundances, they did not affect the outcome of any linear models tested in this study (we ran each model with and without the Seebachtal transects).
Species assemblages of microarthropods and, within these, of collembolans, were mainly driven by soil porosity and organic matter content (Figure 4). Collembolans are detritivores feeding on litter and fungi (Coleman, Callaham, and Crossley 2017) and are thus highly dependent on SOM. Also, species inhabiting the upper soil layer are highly mobile due to their jumping ability and thus rely on a porous soil structure. Oribatid mite communities were driven by soil porosity and silt content. Because they exhibit a large variety of feeding habits (Coleman, Callaham, and Crossley 2017), they are less dependent on organic matter as an entire group, but their dependence on soil porosity has been shown before (Ducarme et al. 2004), because they use the soil pores as living space.

To conclude, species assemblages of microarthropods in snowbeds are rather similar along our west–east transect of the European Alps, because most individuals belong to widespread species. Contrary to our hypotheses, they seem to depend neither on specific soil characteristics nor on the duration of snow cover and the timing of snowmelt. Monitoring these communities and especially the specialists within the communities over a longer period will be necessary to better understand how snowbed invertebrates will respond to a warmer future climate. However, as our data have shown, snowbeds are not suitable as models for larger snowpack duration gradients, as they are for plants, very likely due to the mobility of the animals. Contrary to plants, invertebrates, even (or especially) small ones such as collembolans and oribatid mites, are able to move under snow or away from it if conditions become too harsh.

Disclosure statement

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