



# OPEN Unexpected high subterranean biodiversity on rock glaciers threatened by global warming

José D. Gilgado<sup>1,2</sup>✉, Hans-Peter Rusterholz<sup>2</sup> & Bruno Baur<sup>2</sup>

Global warming is dramatically changing high-alpine plant and animal communities. Rock glaciers serve as habitats for cold-adapted organisms. However, the diversity of subterranean organisms in rock glaciers is still insufficiently understood. We investigated the species richness and abundances of fungi, vascular plants and invertebrates living in the uppermost scree layer on two rock glaciers in the Swiss National Park. As comparison, we investigated the biodiversity of glacier forelands and adjacent lateral scree fields. ITS technique has been used to analyse fungal communities, vegetation surveys for plants and subterranean sampling devices for invertebrates. The number of fungal OTUs on rock glaciers did not differ from values recorded in forelands and lateral scree fields. Species richness of vascular plants was lower on rock glaciers than in their forelands, but higher than in lateral scree fields. A surprisingly high, previously unknown diversity of subterranean invertebrates was discovered in the scree layers: 2 snail, 48 insect and 30 other arthropod species. There were slight but significant differences in the species assemblages of plants and invertebrates between the three habitats. Due to global warming, rock glaciers may disappear, but some alpine scree fields might potentially serve as habitat for cold-adapted organisms in the future.

**Keywords** Cold-adapted organisms, Fungal community, Habitat loss, Invertebrates, Permafrost, Subterranean habitat

Mountain areas are biodiversity hotspots worldwide<sup>1</sup>. This is due to the high rate of local endemism, which is caused by a wide variety of habitats and a combination of habitat isolation and adaptation to cold conditions<sup>2</sup>. However, global warming is currently changing habitats and shifting plant and animal communities<sup>3–5</sup>. This is of particular concern in high mountain regions, where climate warming is progressing two to three times faster than the global average and threatens habitats associated with permafrost, glaciers and seasonal snow<sup>6,7</sup>. The European Alps have experienced particularly rapid warming since the 1980s, which is reflected in the shortened duration of snow cover, the retreat of glaciers and the decline of permafrost areas<sup>8–10</sup>. As warming progresses, permafrost areas will become smaller and, in the long term, all ice-related landforms including glaciers and rock glaciers will lose their permanent ice, thereby reducing the habitat for cold-adapted species<sup>11,12</sup>. Climate refugia are areas large enough to sustain populations of endangered specialized species in the long term while their habitat is lost elsewhere due to climate change<sup>13</sup>. Rock glaciers, debris covered glaciers and related cold rocky landforms could serve as climate refugia for mountain biodiversity in the near future<sup>14–16</sup>.

Rock glaciers are lobe or tongue-shaped landforms composed of a mixture of ice and frozen rock debris that form through gravity-driven creep<sup>17</sup>. The formation of rock glaciers can vary and includes the development of debris-covered glaciers, the formation of ice in rock debris under permafrost conditions and/or the intrusion of water into rock debris and refreezing within the matrix<sup>15,18</sup>. The seasonally frozen layer of debris of varying sizes above the perennially frozen material is commonly a few decimetres to a few metres thick<sup>19</sup>, and provides a cold and stable habitat for fungi, plants and terrestrial invertebrates<sup>15</sup>. The debris cover insulates the ice and thus reduces its melting rate compared to debris-free glaciers<sup>20,21</sup>. Nevertheless, rock glaciers are threatened by global warming<sup>9,22</sup>. In the European Alps, rock glaciers are in different phases of degradation with a general trend of deceleration and loss of volume<sup>22</sup>.

In the present study, we investigated for the first time different groups of organisms (fungi, vascular plants and terrestrial invertebrates) living on and in the debris layer of rock glaciers and compared the biodiversity with those of the glacier forelands and the laterally adjacent scree slopes. With the exception of vascular plants and fungi, the biodiversity of rock glaciers has rarely been explored<sup>13,14</sup>. Various botanical surveys, mainly

<sup>1</sup>Departamento de Ciencias de la Vida, Facultad de Ciencias, Grupo de Investigación de Biología del Suelo y de los Ecosistemas Subterráneos, Universidad de Alcalá, Alcalá de Henares, 28805 Madrid, Spain. <sup>2</sup>Department of Environmental Sciences, University of Basel, 4056 Basel, Switzerland. ✉email: josedomingo.gilgado@uah.es

carried out in the Eastern Alps, show that parts of the debris layer of rock glaciers can be inhabited by a typical high-alpine pioneer vegetation<sup>12,13,23</sup>. Abiotic factors affecting the fungal diversity of rock glaciers have been investigated in the Italian Central Alps<sup>24</sup>. Invertebrates living on the surface of rock glaciers<sup>13,25</sup> and on debris-covered glaciers<sup>26–28</sup> have only been studied sporadically. Within the debris layer is a network of spaces between the rock fragments, the so-called superficial subterranean environment (Milieu Souterrain Superficiel, MSS<sup>29</sup>). The invertebrate communities living underground in the MSS of rock glaciers have not yet been studied. Possible reasons for this are the very remote location of the rock glaciers and the labour-intensive sampling method that must be used.

We investigated the invertebrate communities of the MSS of rock glaciers for the first time. We used subterranean sampling devices (SSDs, vertically buried tubes with side holes and a pitfall trap at the bottom) that operated for 2–3 years to collect invertebrates living in the debris layer. To examine whether the species composition of fungi in the substrate, vascular plants on the surface and invertebrates in the MSS are influenced by habitat characteristics, we recorded the pH and percentage of organic matter (OM) of the fine material, and moss and vascular plant cover at each sampling site.

Due to the underlying ice, different air currents, and snow-cover insulation, the debris layer on the rock glacier is likely to have a lower temperature than the debris layer of the glacier foreland and the adjacent lateral scree slope<sup>13</sup>. Accordingly, we expect different species compositions on rock glaciers than in the glacier forelands and the lateral scree slopes. Using data loggers, we measured the prevailing temperature at a depth of 80 cm in the three habitat types over a period of 1 year.

Our study aimed to answer the following questions: (1) Do the species communities of fungi, vascular plants, and subterranean invertebrates on rock glaciers differ from those in glacier forelands and lateral scree slopes? (2) Can habitat-specific differences in species richness, diversity and composition within the three taxonomical groups of fungi, plants, and invertebrates be explained by habitat characteristics such as elevation, pH, % OM, and moss and vascular plant cover? (3) Are there species that are exclusively typical of rock glaciers, forelands and lateral scree fields and can therefore be considered indicator species for each of the three habitats?

## Materials and methods

### Rock glaciers studied and sampling sites

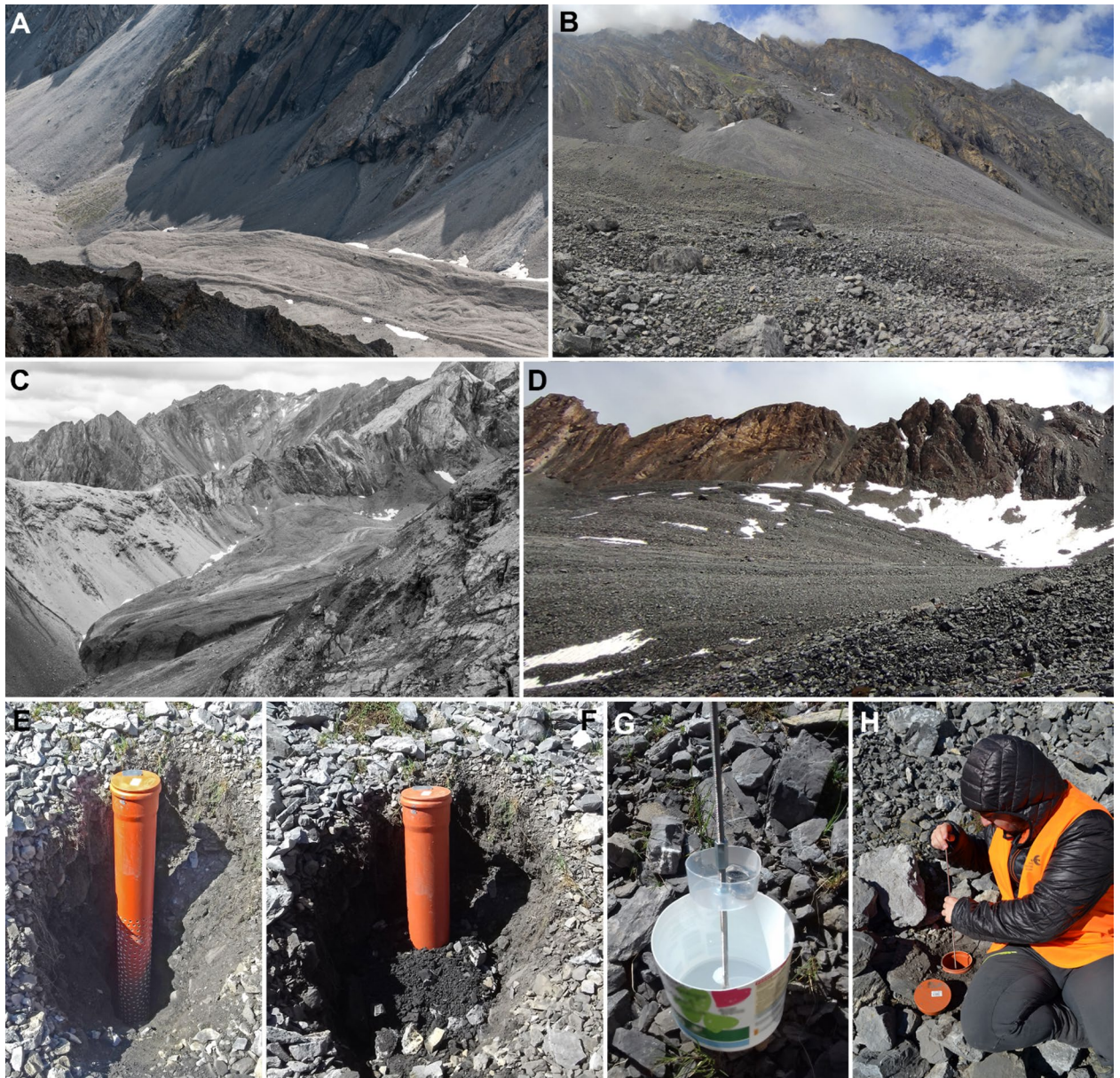
We investigated the debris layers of two rock glaciers, their glacier forelands and lateral scree slopes in two adjacent, parallel valleys in the Swiss National Park (SNP), Eastern Alps, Switzerland (Fig. 1): Val Sassa (46°37'49"N, 10°06'46"E) and Valletta (46°38'20"N, 10°06'09"E). The Swiss National Park is a strict nature reserve (category Ia<sup>30</sup>) with no habitat and wildlife management. Access to the SNP is only allowed on marked trails during summer<sup>31</sup>. The bedrock in the study region is dolomite<sup>32</sup>.

Rock glaciers are typically divided into two main categories based on their surface movement: active or inactive<sup>33</sup>. Surface movement in active rock glaciers can be due to various processes, such as permafrost creep, hydrological changes, and solifluction. These often vary greatly from point to point, resulting in highly heterogeneous patterns of movement intensity<sup>34</sup>. Both the Val Sassa and Valletta rock glaciers are active<sup>22</sup>.

The Val Sassa rock glacier is 1200 m long, 150–200 m wide, and its N-facing lobe extends from 2100 to 2600 m a.s.l. with an average slope of 23.5%<sup>22</sup>. The Val Sassa rock glacier shows a significant deceleration. Its velocity decreased from 2 m/year in 1918–1919 to 5–7 cm/year in 2000–2019<sup>22</sup>. This deceleration coincides with an on-going substantial volume loss of 60,000 m<sup>3</sup>/year<sup>22</sup>. The Valletta rock glacier is 700 m long and 350 m wide. Its tongue-shaped lobe faces to north and extends from 2490 to 2660 m a.s.l. with an average slope of 22%<sup>22</sup> (Fig. 1A–D). This rock glacier exhibited the highest historical velocity of 2.5 m/year in the SNP in 1946–1956<sup>22</sup>. Since then, its velocity has decreased to 1.2 m/year in 2000–2019<sup>22</sup>. The reduction in velocity is accompanied by a general volume loss. Both rock glaciers were spatially connected to glaciers at the end of the Little Ice Age (in 1850, Dufour map, official topographical map of Switzerland<sup>35</sup>). At that time, the upper part of the Valletta rock glacier was covered by a glacier (sampling sites VR3, VR4 and VL2; Fig. 2C), and in 2022, remnants of bare glacier ice can still be seen in the uppermost part of the rock glacier<sup>22</sup>. The part of the Val Sassa rock glacier we studied was not covered by the glacier in 1850. In the scree layer of the two rock glaciers studied, the permafrost boundary lies at a depth of 4–7 m<sup>22</sup>.

In our study, we considered the debris layer of the rock glacier, the glacier foreland and the adjacent scree slope as three different habitat types, although they consist of the same rock type (dolomite). The forelands in the front of the rock glaciers are characterized by an increased humidity due to melting water and a reduced temperature that flows out from the ice of the rock glacier. The forelands show spatially varying amounts of fine sediment and a patchy plant cover. Lateral scree fields cover the steep talus slopes. The scree fields consist mainly of coarse debris, which creates large interstitial voids between the rocks and limits the establishment of vegetation. These talus slopes typically develop internal air currents that provide cool subsurface temperatures with seasonal variations<sup>15</sup>.

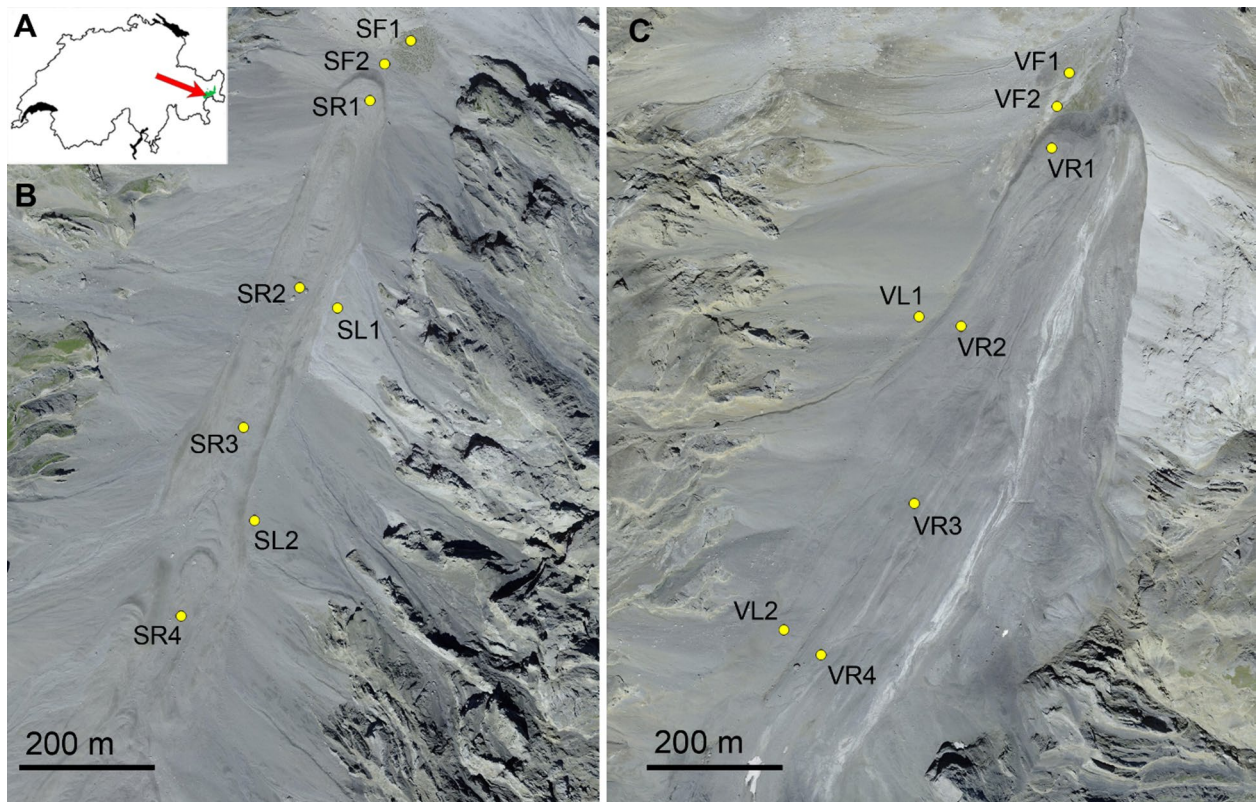
We selected eight sampling sites in Val Sassa (S) and eight in Valletta (V). The location of a sampling site is defined by the SSD installed (see Invertebrate survey). Four sampling sites arranged in a line were located on each of the two rock glaciers: one close to the end of the lobe (R1), the others at distances of 200–300 m from each other up the rock glacier (R2–R4; Fig. 2B and C). The elevation range of the four sampling sites was 2120–2300 m in Val Sassa and 2530–2690 m in Valletta. Two sampling sites were chosen in the foreland of each rock glacier: one 30 m from the front of rock glacier lobe (F2) and one at a distance of 70 m (F1; Fig. 2). In both valleys, the foreland sampling sites had not been covered by ice for more than 50 years. Another two sampling sites were chosen in the adjacent lateral scree fields of each rock glacier at a distance of 15–20 m from the glaciers (L1 and L2; Fig. 2). The distance between these two sampling sites was 340 m in Val Sassa and 500 m in Valletta. Coordinates and elevation of the sampling sites are presented in Table S1.



**Fig. 1.** Surveyed rock glaciers and invertebrate sampling methodology. (A) Val Sassa rock glacier (Foto H. Lozza, SNP). (B) Surface of Val Sassa rock glacier. (C) Valletta rock glacier (Foto H. Lozza, SNP). (D) Surface of Valletta rock glacier. (E) The Subterranean Sampling Device (SSD) tube was inserted in the freshly dug hole shortly before it was covered. (F) The partially buried tube during the installation process. (G) Pitfall trap, with metal rod, and platform with thermometers. (H) The metal rod can be used to retrieve the pitfall trap.

### Sampling of soil fungal community

We sampled substrate 1 m from each SSD in August 2021. The surface layer of rock glaciers consists of rock fragments of varying sizes on the surface, beneath which lies a fine-grained layer with a relatively high proportion of fine material. Using a small shovel and a spade, we obtained samples of fine material, which consisted of organic material, sand and gravel of different size that had accumulated in the crevices between stones of various size. Due to the absence of visible soil horizons, samples were taken at five depths: 0–5 cm, 6–10 cm, 11–20 cm, 21–50 cm, and 51–75 cm. To avoid mixing and contamination of samples taken from different depths, the shovel and spade were cleaned with ethanol between each sample. At each depth, 10–25 g fine material was collected and stored in an individual paper bag. The samples were dried for 10 days at room temperature. This drying procedure is the most suitable method for assessing soil fungal communities collected in remote locations<sup>36</sup>. Overall, our sampling schedule resulted in 80 samples (2 valleys × 8 sampling sites × 5 depths). In the laboratory, we sieved the samples (mesh size 2 mm) for further analyses.



**Fig. 2.** Location of sampling sites. (A) Outline of Switzerland; the Swiss National Park is marked in green, and the red arrow points to the studied rock glaciers. (B) Aerial view of Val Sassa rock glacier (north at the top). (C) Aerial view of Valletta rock glacier (north at the top). The sampling sites and their codes are indicated. Aerial photographs © swisstopo.

### DNA-extraction and fungal community determination

We extracted total genomic DNA from 0.45 to 0.55 g of sieved fine material samples in triplicate using NucleoSpin Soil kit (Macherey-Nagel, Oensingen, Switzerland) according to the manufacturer's instructions. The triplicate DNA extracts were combined into one sample and purified using NucleoSpin gDNA Clean-up kit (Macherey-Nagel, Oensingen, Switzerland). We first checked whether DNA could be successfully extracted from the samples using agarose gels. We then determined the DNA concentration and quality using NanoDrop (NanoDrop Technologies Inc., Wilmington, NC, USA), adjusted the DNA concentration to 5–10 ng/ $\mu$ L, and stored the samples at  $-20^{\circ}\text{C}$ . Of the 80 samples, DNA was successfully extracted from 76 samples (95%).

We determined fungal communities by amplifying the internal transcribed spacer 2 region (ITS2) with the primer pair ITS3, which is fluorescently labelled at the 5'-end (FAM), and ITS4<sup>37</sup>. PCR reactions (40  $\mu$ L) consisted of 10  $\mu$ L template DNA, 8  $\mu$ L Master Mix (5x FIREPOL Master Mix, Solis BioDyne, Estonia), 1  $\mu$ L Primer ITS3-F (10  $\mu$ M), 1  $\mu$ L Primer ITS4 (10  $\mu$ M), and 20  $\mu$ L sterile water. Amplification was achieved in an Eppendorf Mastercycler Pro (Vaudaux-Eppendorf AG, Schönenbuch, Switzerland) under the following conditions: initial 5 min. heat activation step at  $95^{\circ}\text{C}$ , followed by 35 amplification cycles of denaturation at  $95^{\circ}\text{C}$  for 60 s, annealing at  $55^{\circ}\text{C}$  for 60 s, and extension at  $72^{\circ}\text{C}$  for 90 s, with a final extension step at  $72^{\circ}\text{C}$  for 7 min. All PCR reactions were performed in triplicate. The pooled PCR products were purified using the NucleoSpin gDNA Clean-up kit (Macherey-Nagel, Oensingen, Switzerland). Samples were prepared as GeneScan samples (1.5  $\mu$ L DNA sample (20 ng/ $\mu$ L); 1.5  $\mu$ L GeneScan 1200LIZ size standard; 17  $\mu$ L Hi-Di Formamide; Applied Biosystems, LifeTechnologies). Fragment analysis was conducted by MacroGen Inc. (Amsterdam, The Netherlands), by resolving the PCR products on a capillary sequencer (ABI 3730 XL DNA Analyser). The size of the fluorescent amplified fragments was quantified using Peak Scanner software (version 1.0, Applied Biosystems, Inc., Massachusetts, USA). Peaks with a size of 390 to 1000 bp were considered in the analyses<sup>38</sup>, and peak sizes were rounded to the nearest base pair<sup>39</sup>. To avoid possible background noise, only peaks with a signal above 1% of the sum of all peak areas were included in the analyses<sup>40</sup>. Peaks that differed in size by more than 2.0 bp were each considered as a separate fungal OTU<sup>41</sup>. We calculated the average of the fungal data from the five depths per sampling site for later data analysis.

### Plant survey

To assess the richness and composition of vascular plant species, we established three sampling plots measuring 2 m  $\times$  2 m at each sampling site, spaced 2 m from the SSD. In all plots, we recorded each plant species and visually estimated its cover using the Braun-Blanquet scale<sup>42</sup>. In addition, we estimated the overall cover of

mosses (in %, species not determined) in each sampling plot using the same scale as for plants. Plants were recorded in a total of 48 plots (2 valleys  $\times$  8 sampling sites  $\times$  3 plots). Plant species were identified following Lauber et al.<sup>43</sup>. Vegetation survey was carried out during the flowering peak of the alpine plants in August 2021. For the data analysis, the average of the three sampling plots per site was calculated for plant cover and Shannon diversity index, and the cumulative number of vascular plant species of the three sampling plots was used for plant species richness per site.

### Invertebrate survey

We installed one SSD per sampling site to capture invertebrates living in the subterranean habitat (Fig. 1E–H). An SSD consists of a 1 m long PVC tube, 11 cm in diameter, buried vertically in the ground with the upper end at surface level. Each tube has numerous lateral perforations (each 8 mm in diameter) below the first 40 cm, which allow invertebrates to enter the interior of the tube (Fig. 1E). A pitfall trap containing propylene glycol, without bait, was placed at the bottom of each tube to record invertebrate activity while avoiding biases such as attracting epigeal decomposers (Fig. 1G). During each visit, the pitfall trap was retrieved by means of an attached metal rod (Fig. 1G and H), emptied and refilled with propylene glycol. We installed the SSDs in July 2019 (Val Sassa) and August 2020 (Valletta). We emptied the traps twice a year, in early and late summer, until the last visit in September 2022 (maximum operating period 1140 days in Val Sassa and 761 days in Valletta). Dates of trap installation and trap emptying are presented in Table S2.

The captured invertebrates were sorted into taxonomic groups and preserved in ethanol. Individuals from ten taxonomic groups were identified to species by experts: Araneae by Ambros Hänggi, Opiliones by Karin Urfer and Carlos Prieto, Pseudoscorpionida by Jana Christophoryová and Katarína Krajčovičová, Chilopoda by David Cabanillas, Diplopoda by José D. Gilgado, Collembola by Jörg Salamon, Diplura by Alberto Sendra, Carabidae by Yannick Chittaro and José D. Gilgado, Staphylinidae by Alexander Szallies, and Gastropoda by Bruno Baur and Jörg Rüetschi. Informed consent was obtained from the experts. Beetle larvae were not identified. Because of the very large number of Collembola caught (>45,000 individuals), only subsamples consisting of a total of 3,900 individuals were identified to the species. Juveniles or broken individuals that could only be determined to genus or family level were only considered when it was clear that they constituted an additional taxon. Voucher specimens from all species are stored in the collection of the Bündner Naturmuseum Chur (BNM), Switzerland.

Based on literature data, the invertebrate species found were assigned to one of the following functional feeding groups (trophic niches; Table S3): predators, herbivores, decomposers and generalists (if they belonged to two different groups). Saprophagous, microbivorous, and fungivorous species were all considered decomposers.

### Habitat characteristics

To record the temperature in each SSD, we placed two thermometers (Thermobutton 22 L, Plug&Track, Lille, France) on a small platform attached to the metal rod of each pitfall trap, located at a depth of 80 cm inside the tube (Fig. 1G). The thermometers took air temperature measurements every three hours. In our study we used data over one year (from 21 August 2020 to 13 July 2021). The thermometers were recovered and replaced by new ones, at each visit, and the data were downloaded using Thermo-Track PC (Plug&Track, Lille, France). We combined the data from the two data loggers in each tube and calculated the average temperature for each sampling site in the two valleys over the year (Fig. 3). From the measurement data, we also extracted the number of days during the year when the temperature was 0 °C or lower. However, this number of days was highly significantly correlated with the annual average temperature ( $r_s = -0.891$ ,  $n = 16$ ,  $P < 0.0001$ ). Therefore, we only used the average temperature in the data analyses. For illustrative purposes, we also measured the temperature in the tubes at two sampling sites in Valletta (VR1 and VF2) with the same type of thermometers at surface level and at depths of 20, 40, 60 and 80 cm (Fig. 4). Surface thermometers were covered with stones to prevent overheating produced in the debris by solar radiation<sup>44</sup>.

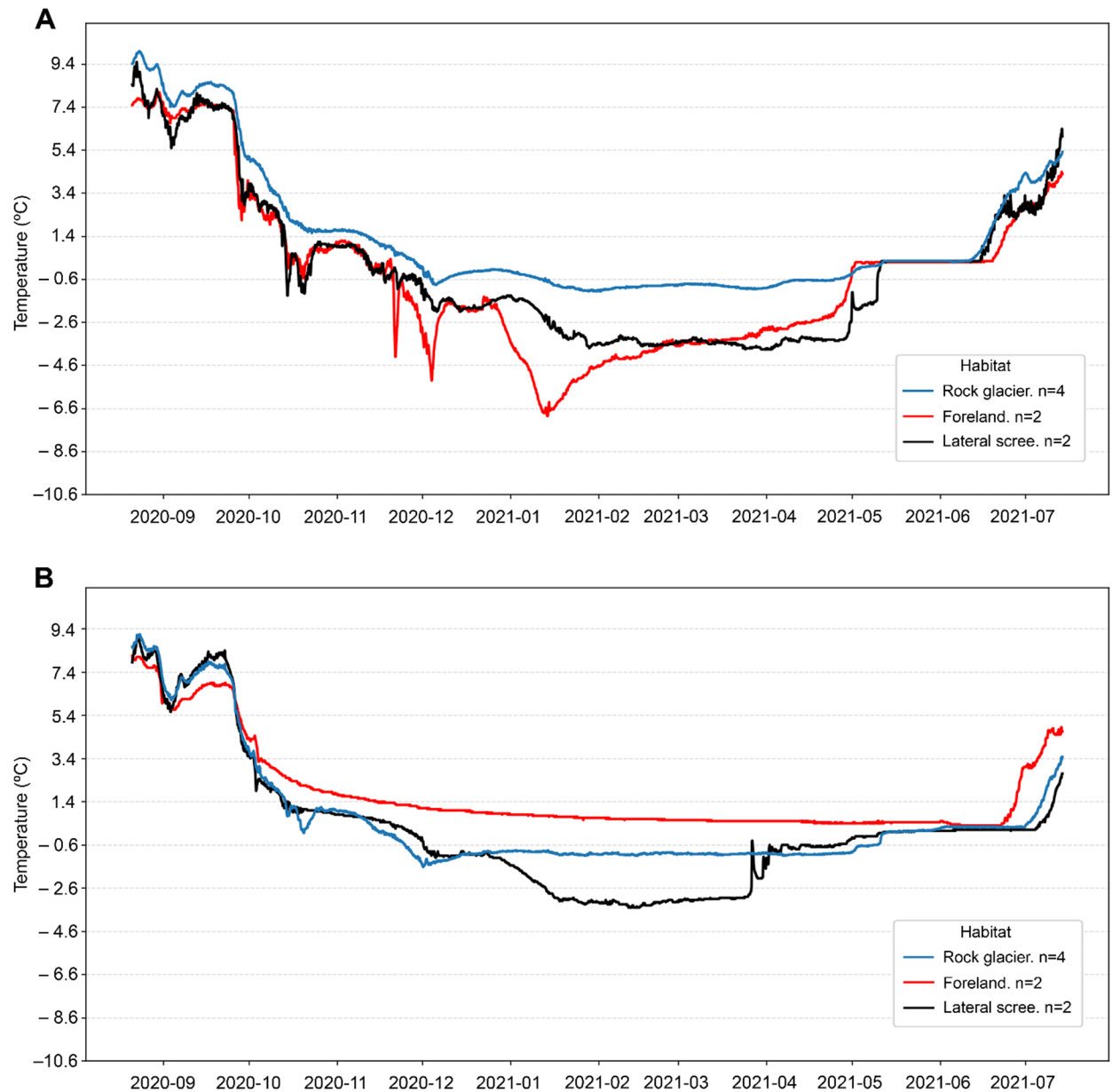
The following ecological variables were assessed at each sampling site (Table S1). We measured the elevation (in metres above the sea level) with a GPS receiver Garmin Gecko 201 (Garmin, Southampton, U.K.). We estimated the total cover of vascular plants and mosses (mean value of the three 2 m  $\times$  2 m plots). We determined the pH of the sieved fine material in distilled water (1:2.5 soil: water) and the total organic matter content (OM, %) as the loss-on-ignition of oven-dried fine material at 750 °C for 16 h<sup>45</sup> and calculated the mean value of the samples taken at the five different depths (see: Sampling of soil fungal community).

### Data analyses

We performed all statistical analyses in the R environment<sup>46</sup>. We considered the sampling sites (i.e., the location of an SSD) as unit of the data analysis ( $n = 16$ ). The number of species found and their abundances at the 16 sampling sites are listed in Table S3 (invertebrates), Table S4 (fungi, OTUs), and Table S5 (vascular plants). We assumed that the different invertebrate groups differ in their preference for the ecological conditions existing in the specific habitat type. Therefore, we conducted separate analyses for the groups “all invertebrates”, “arthropods excluding insects”, and “only insects”. The division into these groups was chosen because “arthropods excluding insects” mainly consists of myriapods, while the group “all invertebrates” also includes gastropods.

We used individual-based rarefied species richness to consider the large variation in number of fungal OTUs and the number of invertebrate individuals of the three groups (all invertebrates, arthropods excluding insects, and insects) among the sampling sites with the *iNEXT* package<sup>47</sup>. The Shannon diversity and Pielou's evenness index indices of the species groups were calculated using the *vegan* package<sup>48</sup>.

We applied general linear models (GLM) with Gaussian distribution to examine potential effects of valley, habitat type, elevation, mean temperature, vascular plant and moss cover, pH, and OM of the fine debris material on the number of observed and rarefied fungal OTUs, Shannon diversity and Pielou's evenness index of the fungal OTUs. For vascular plants, we used the same GLM-model to analyse observed plant species richness

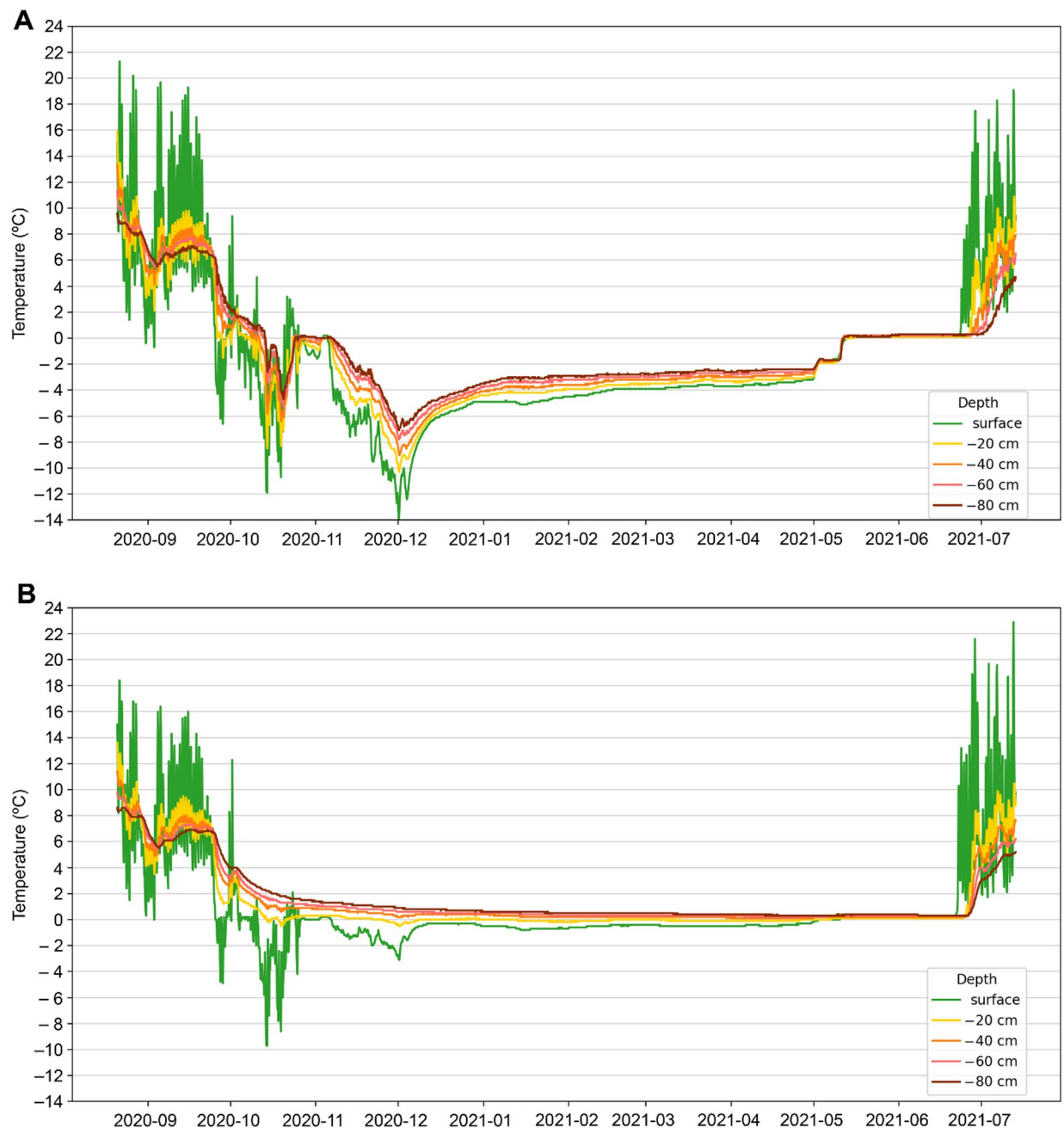


**Fig. 3.** Mean temperatures measured in the SSDs at a depth of 80 cm from 21 August 2020 to 13 July 2021 in three habitat types (rock glacier, foreland and lateral scree field) in (A) Val Sassa and (B) Valletta.

and the two diversity indices. Similarly, the same GLM model was applied for the observed and rarefied species richness, abundance (expressed as number of individuals per 100 trapping days) and the two diversity indices of the three invertebrate groups. For analyses, observed and rarefied species richness and abundance were log-, sqrt- or Tuckey-transformed. The Shannon diversity and Pielou's evenness index were sqrt- or Tuckey-transformed, vascular plant and moss cover were arcsine sqrt-transformed and OM was Tukey-transformed. All GLM models were reduced using the stepwise model reduction procedure. The fits of different models were compared using the AIC-weight approach<sup>49</sup>.

We used permutational multivariate analyses of variance (PERMANOVA) to test whether valley, habitat type and habitat characteristics affected species composition of fungi, vascular plants, all invertebrates, arthropods excluding insects and insects<sup>50</sup>. Habitat characteristics were included as co-factors. All PERMANOVA tests were based on 999 permutations of the untransformed raw data, using the *adonis*-function in the *vegan* package<sup>48</sup>. We used non-metric multidimensional scaling (NMDS) with Bray-Curtis dissimilarity measures to illustrate differences in species composition of fungi, vascular plants, all invertebrates, arthropods excluding insects, and insects between valleys and habitat types. Data were square-root-transformed and Wisconsin double standardization was applied using the *vegan* package<sup>48</sup>.

We performed a hierarchical cluster analysis to visualize the species associations of the invertebrates at the sampling site level. We used the Ward method with Euclidean distances in the *hclust* function of the *vegan*



**Fig. 4.** The temperatures measured in two SSDs at depths of 0, 20, 40, 60 and 80 cm in the scree layer of the rock glacier Valletta (A) and in its foreland (B) from 21 August 2020 to 13 July 2021.

package<sup>48</sup>. The *hclust* function uses pairwise dissimilarities between species. The Ward clustering method is based on the sum of squares and minimizes the within-group dispersion in each binary fusion step<sup>51</sup>. We used the silhouette method to assess the number of selected groups<sup>51</sup>.

We used the Chi-square test to examine whether the three habitat types rock glacier, foreland and lateral scree field differed in the percentage composition of the functional feeding groups of the invertebrates. Data from the Val Sassa and Valletta valleys were combined for this analysis and the species were weighted based on the number of individuals caught. Species whose functional group is unknown were not included in the analysis.

Using the *indicspecies* package<sup>52</sup>, we conducted an indicator species analysis to identify species associated with a given habitat type (scree layer of rock glacier, foreland, and lateral scree field).

## Results

### Species richness and abundance

In total, we found 64 fungal OTUs in the two valleys (Table S4). The number of OTUs detected did not differ between the two valleys (Tables 1 and 2; Val Sassa 60, Valletta 57). Furthermore, the three habitat types studied

	Val Sassa			Valletta		
	Rock glacier	Foreland	Lateral scree	Rock glacier	Foreland	Lateral scree
<b>Fungi (64 OTUs)</b>						
Number of OTUs	10.35 ± 2.19	16.57 ± 3.30	15.10 ± 2.58	12.65 ± 2.06	13.20 ± 2.80	14.50 ± 3.39
Rarefied number of OTUs	9.95 ± 1.99	14.96 ± 2.59	14.62 ± 2.48	11.95 ± 1.83	12.32 ± 2.88	14.09 ± 3.17
Shannon diversity index	1.51 ± 0.16	1.63 ± 0.27	2.00 ± 0.16	1.74 ± 0.17	1.52 ± 0.26	1.98 ± 0.22
Evenness	0.83 ± 0.09 <sup>a</sup>	0.68 ± 0.09 <sup>b</sup>	0.83 ± 0.05 <sup>a</sup>	0.80 ± 0.04	0.69 ± 0.06	0.85 ± 0.05
<b>Vascular plants (36 sp.)</b>						
Species richness	4.84 ± 0.35 <sup>a</sup>	7.85 ± 3.17 <sup>a</sup>	0.00 <sup>b</sup>	1.84 ± 0.29 <sup>a</sup>	6.33 ± 1.00 <sup>b</sup>	1.00 ± 0.50 <sup>a</sup>
Vegetation cover (%)	7.88 ± 1.21	24.84 ± 20.27	0.00	2.75 ± 0.30 <sup>a</sup>	8.50 ± 0.17 <sup>b</sup>	0.63 ± 0.38 <sup>c</sup>
Shannon diversity index	1.07 ± 0.11	1.07 ± 0.19	–	0.31 ± 0.13 <sup>a</sup>	1.17 ± 0.15 <sup>b</sup>	0.05 ± 0.03 <sup>a</sup>
Evenness	0.77 ± 0.04 <sup>a</sup>	0.54 ± 0.02 <sup>b</sup>	–	0.80 ± 0.06 <sup>a</sup>	0.62 ± 0.07 <sup>a</sup>	0.03 ± 0.03 <sup>b</sup>
<b>Invertebrates (80 species)</b>						
Species richness	24.25 ± 1.80	31.00 ± 5.00	20.50 ± 2.50	14.00 ± 1.78	16.00 ± 1.00	19.00 ± 3.00
Rarefied species richness	26.78 ± 2.53	34.45 ± 3.93	23.23 ± 1.23	16.38 ± 2.51	19.58 ± 2.50	20.87 ± 3.76
Abundance <sup>1</sup>	42.43 ± 10.05	46.05 ± 15.00	53.30 ± 24.70	47.62 ± 2.48	25.38 ± 17.32	63.83 ± 17.77
Shannon diversity index	2.02 ± 0.08	2.02 ± 0.30	2.01 ± 0.19	1.50 ± 0.16	2.11 ± 0.14	1.63 ± 0.23
Evenness	0.64 ± 0.02	0.59 ± 0.06	0.67 ± 0.09	0.58 ± 0.05	0.77 ± 0.07	0.55 ± 0.05
<b>Arthropods excluding insects (30 species)</b>						
Species richness	9.50 ± 0.65	13.50 ± 1.50	8.50 ± 1.50	4.75 ± 0.48	3.50 ± 0.50	8.00 ± 2.00
Rarefied species richness	10.68 ± 0.90	14.69 ± 0.74	10.27 ± 0.40	4.96 ± 0.59	3.50 ± 0.48	8.02 ± 1.98
Abundance <sup>1</sup>	6.22 ± 0.54	11.58 ± 8.33	9.09 ± 6.79	28.02 ± 1.95	8.73 ± 4.26	33.03 ± 0.35
Shannon diversity index	1.76 ± 0.16	1.77 ± 0.41	1.69 ± 0.04	0.38 ± 0.14	0.89 ± 0.09	0.57 ± 0.07
Evenness	0.79 ± 0.08	0.69 ± 0.19	0.80 ± 0.09	0.24 ± 0.08	0.74 ± 0.16	0.28 ± 0.01
<b>Insects (48 species)</b>						
Species richness	14.25 ± 0.85	17.00 ± 4.00	11.04 ± 1.00	9.00 ± 1.58	11.00 ± 1.00	11.00 ± 1.00
Rarefied species richness	17.27 ± 2.38	20.02 ± 3.17	11.15 ± 1.10	11.24 ± 2.77	15.34 ± 1.38	12.72 ± 2.54
Abundance <sup>1</sup>	35.86 ± 10.00	34.38 ± 6.67	45.26 ± 18.86	19.43 ± 3.31	16.22 ± 13.24	30.15 ± 16.67
Shannon diversity index	1.53 ± 0.04	1.56 ± 0.28	1.63 ± 0.29	1.51 ± 0.09	1.83 ± 0.26	1.51 ± 0.01
Evenness	0.58 ± 0.02	0.55 ± 0.05	0.69 ± 0.15	0.71 ± 0.03	0.77 ± 0.14	0.63 ± 0.02

**Table 1.** Diversity and abundance measures of fungi, vascular plants and invertebrates (with arthropods excluding insects and insects listed separately) in the debris layers of rock glaciers, glacier forelands and lateral scree fields in two neighbouring valleys (Val Sassa and Valletta) in the Eastern Alps, Switzerland. Number in brackets indicate total number of species detected in the different species groups. Mean values ± s.e. are given ( $n = 16$  in each case). Different letters indicate significant differences between habitat types ( $P < 0.05$ ). <sup>1</sup>Abundance is expressed as number of individuals per 100 trapping days.

within the valley did not differ in any of the diversity measures considered, with the exception that fungal evenness was lower in the foreland than in the rock glacier scree layer and the lateral scree field in Val Sassa (Table 1).

We recorded 26 vascular plant species in Val Sassa and 19 species in Valletta (36 species in total; Table S5). The two valleys differed both in plant species richness and Shannon diversity (Tables 1 and 2). In both valleys, the three habitat types differed in almost all diversity measures (Table 2). Glacier forelands had the largest vegetation cover (8.5–24.8%) and the highest plant species richness (Table 1). Vegetation cover was lower on the two rock glaciers (2.7–7.8%; Table 1). A moderate plant species richness was found in the scree layer of the two rock glaciers, while no plants (Val Sassa) and only two species (Valletta) were detected in the lateral scree fields.

Using SSDs, we were able to detect individuals of a total of 80 invertebrate species (Val Sassa 68, Valletta 42; Table S3). The invertebrates found in the traps included Gastropoda (2 species), Araneae (14), Opiliones (2), Pseudoscorpionida (2), Chilopoda (4), Diplopoda (8), Collembola (19), Diplura (1), and the Coleopteran families Carabidae (3) and Staphylinidae (25). Val Sassa had a higher invertebrate species richness, rarefied species richness and Shannon diversity index than Valletta (Tables 1 and 2). However, the two valleys did not differ in invertebrate abundance (number of individuals captured per 100 trapping days) and evenness (Table 2). Interestingly, the three habitat types did not differ in any invertebrate diversity measures or invertebrate abundance (Table 2).

In the further analyses, we considered the two groups “arthropods excluding insects” (30 species) and “insects” (48 species) separately. Val Sassa had a higher “arthropod excluding insects” species richness, rarefied species richness, Shannon diversity index and evenness than Valletta (Tables 1 and 2). In contrast, “arthropod excluding insects” abundance was higher in Valletta than in Val Sassa (Table 2). Furthermore, the three habitat types did not differ in any arthropod diversity measures or arthropod abundance (Table 1).

Fungi (64 OTUs)	Valley	Habitat	Elevation	Mean temperature	Moss cover
Number of OTUs	$F_{1,14} = 0.01, P = 0.945$	$F_{2,12} = 2.22, P = 0.159$	$F_{1,11} = 2.84, P = 0.122$	$F_{1,10} = 3.50, P = 0.091$	–
Rarefied number of OTUs	$F_{1,14} = 0.01, P = 0.911$	$F_{2,12} = 2.33, P = 0.142$	$F_{1,11} = 2.19, P = 0.169$	$F_{1,10} = 1.98, P = 0.189$	–
Shannon diversity index	$F_{1,14} = 0.27, P = 0.616$	$F_{2,12} = 3.07, P = 0.087$	–	–	$F_{1,11} = 1.83, P = 0.203$
Evenness	$F_{1,14} = 0.05, P = 0.836$	$F_{2,12} = 10.99, P = 0.002$	$F_{1,11} = 4.76, P = 0.053$	–	–
<b>Vascular plants (36 sp.)</b>					
Species richness	$F_{1,14} = 5.28, P = 0.049$	$F_{2,12} = 66.46, P < 0.001$	–	$F_{1,11} = 9.18, P = 0.016$	–
Shannon diversity index	$F_{1,12} = 28.90, P = 0.001$	$F_{2,10} = 10.38, P = 0.008$	–	$F_{1,9} = 9.94, P = 0.018$	$F_{1,8} = 1.92, P = 0.208$
Evenness	$F_{1,14} = 0.01, P = 0.934$	$F_{2,12} = 11.74, P = 0.003$	–	–	–
<b>Invertebrates (80 species)</b>					
Species richness	$F_{1,14} = 32.31, P < 0.001$	$F_{2,12} = 2.51, P = 0.142$	–	–	$F_{1,11} = 6.44, P = 0.034$
Rarefied species richness	$F_{1,14} = 25.91, P < 0.001$	$F_{2,12} = 3.01, P = 0.100$	–	–	$F_{1,11} = 6.58, P = 0.030$
Abundance <sup>1</sup>	$F_{1,14} = 0.01, P = 0.993$	$F_{2,12} = 3.51, P = 0.081$	$F_{1,11} = 11.67, P = 0.009$	–	$F_{1,10} = 5.31, P = 0.050$
Shannon diversity index	$F_{1,14} = 10.97, P = 0.013$	$F_{2,12} = 3.41, P = 0.093$	–	–	$F_{1,11} = 3.82, P = 0.092$
Evenness	$F_{1,14} = 0.23, P = 0.641$	$F_{2,12} = 1.61, P = 0.360$	–	–	–
<b>Arthropods excluding insects (30 species)</b>					
Species richness	$F_{1,14} = 100.42, P < 0.0001$	$F_{2,12} = 2.31, P = 0.169$	–	$F_{1,11} = 9.63, P = 0.017$	$F_{1,10} = 16.08, P = 0.005$
Rarefied species richness	$F_{1,14} = 82.86, P < 0.0001$	$F_{2,12} = 1.61, P = 0.266$	–	$F_{1,11} = 6.87, P = 0.034$	$F_{1,10} = 6.37, P = 0.040$
Abundance <sup>1</sup>	$F_{1,14} = 32.74, P < 0.001$	$F_{2,12} = 2.75, P = 0.123$	–	$F_{1,11} = 2.19, P = 0.178$	$F_{1,10} = 18.03, P = 0.003$
Shannon diversity index	$F_{1,14} = 72.47, P < 0.0001$	$F_{2,12} = 1.48, P = 0.265$	–	–	$F_{1,11} = 3.62, P = 0.084$
Evenness	$F_{1,14} = 36.42, P < 0.001$	$F_{2,12} = 3.43, P = 0.078$	–	$F_{1,11} = 5.53, P = 0.043$	$F_{1,10} = 12.66, P = 0.006$
<b>Insects (48 species)</b>					
Species richness	$F_{1,14} = 14.20, P = 0.004$	$F_{2,12} = 1.74, P = 0.230$	–	–	$F_{1,11} = 4.58, P = 0.060$
Rarefied species richness	$F_{1,14} = 4.19, P = 0.067$	$F_{2,12} = 2.55, P = 0.128$	–	–	$F_{1,11} = 3.76, P = 0.081$
Abundance <sup>1</sup>	$F_{1,14} = 9.43, P = 0.011$	$F_{2,12} = 1.39, P = 0.294$	$F_{1,11} = 12.77, P = 0.005$	–	–
Shannon diversity index	$F_{1,14} = 0.06, P = 0.817$	$F_{2,12} = 0.98, P = 0.411$	–	$F_{1,11} = 7.35, P = 0.024$	$F_{1,10} = 1.50, P = 0.253$
Evenness	$F_{1,14} = 5.44, P = 0.042$	$F_{2,12} = 0.04, P = 0.957$	–	$F_{1,11} = 2.42, P = 0.152$	–
	<b>Plant cover</b>	<b>pH</b>	<b>OM</b>	<b>Valley x habitat</b>	
<b>Fungi (64 OTUs)</b>					
Number of OTUs	–		–	–	
Rarefied number of OTUs	–		–	–	
Shannon diversity index	–		–	–	
Evenness	–		–	–	
<b>Vascular plants (36 sp.)</b>					
Species richness		$F_{1,10} = 8.97, P = 0.017$	–	$F_{2,8} = 8.44, P = 0.011$	
Shannon diversity index	$F_{1,7} = 3.36, P = 0.109$		–	–	
Evenness	–		–	–	
<b>Invertebrates (80 species)</b>					
Species richness	–	$F_{1,10} = 3.53, P = 0.097$	–	$F_{2,8} = 3.21, P = 0.095$	
Rarefied species richness	–		–	$F_{2,9} = 3.28, P = 0.085$	
Abundance <sup>1</sup>	–	$F_{1,9} = 4.71, P = 0.075$	$F_{1,8} = 2.28, P = 0.169$	–	
Shannon diversity index	–	$F_{1,10} = 3.73, P = 0.095$	$F_{1,9} = 2.58, P = 0.152$	$F_{2,8} = 4.55, P = 0.054$	
Evenness	–	$F_{1,11} = 5.96, P = 0.040$	$F_{1,10} = 2.72, P = 0.137$	$F_{2,8} = 2.39, P = 0.154$	
<b>Arthropods excluding insects (30 species)</b>					
Species richness	$F_{1,9} = 10.83, P = 0.012$		–	$F_{2,7} = 10.39, P = 0.007$	
Rarefied species richness	$F_{1,9} = 5.23, P = 0.056$		–	$F_{2,7} = 4.22, P = 0.062$	
Abundance <sup>1</sup>	$F_{1,9} = 5.44, P = 0.047$	$F_{1,8} = 2.45, P = 0.156$	–	–	
Shannon diversity index	–		–	–	
Evenness	–	$F_{1,9} = 3.77, P = 0.084$	–	–	
<b>Insects (48 species)</b>					
Continued					

	Plant cover	pH	OM	Valley x habitat	
Species richness	–		–	$F_{2,9} = 3.76, P = 0.065$	
Rarefied species richness	–		$F_{1,10} = 4.03, P = 0.072$	–	
Abundance <sup>1</sup>	–	$F_{1,10} = 1.87, P = 0.201$	–	–	
Shannon diversity index	–	$F_{1,9} = 1.59, P = 0.239$	–	–	
Evenness	–	$F_{1,10} = 3.86, P = 0.078$	–	–	

**Table 2.** Results of the GLM analyses examining potential effects of valley, habitat and their interaction, elevation, mean temperature, moss and vascular plant cover, pH and OM of the fine material on species richness, abundance, Shannon diversity and evenness of fungi, vascular plants and invertebrates in the debris layers of three habitats (rock glacier, foreland and lateral scree) in two neighbouring valleys (Val Sassa and Valletta) in the Eastern Alps, Switzerland. Significant *P*-values (<0.05) are indicated in bold.

If we consider only the 48 insect species, the two valleys differed in species richness, Shannon diversity and abundance (Tables 1 and 2). As with non-insect arthropods, there were no differences in insect diversity or abundance among the three habitat types (Table 2).

### Temperature and effects of habitat characteristics on diversity measures

The scree layer dampens daily temperature fluctuations (Fig. 3). Regarding the temperature at different depths, daily fluctuations of  $-2$  to  $21$  °C were measured in the scree surface layer of the rock glacier during the snow-free period (Fig. 4A). In the scree layer at a depth of 20 cm, daily fluctuations of 2 to 12 °C were recorded; at a depth of 80 cm, daily fluctuations were less than 1 °C (Fig. 4A). The lowest temperatures in the scree layer were measured in the Valletta rock glacier in November, before an abundant snow cover was present (Fig. 4A). The minimum temperature in November was  $-14$  °C at the surface of the scree layer, but only  $-7$  °C at a depth of 80 cm (Fig. 4A). Once the rock glacier was covered with snow, the temperature varied between  $-5$  and  $-4$  °C at the surface of the scree layer, while at a depth of 80 cm it was around  $-2$  °C (Fig. 4A). Thus, during the winter, the temperature in the scree layer at a depth of 80 cm was higher than in the surface layer. A similar annual temperature variation at different depths in the scree layer was measured in the glacier foreland (Fig. 4B), although temperatures there were slightly higher during winter compared to the temperatures in the rock glacier (Fig. 4A). In the following analyses, we considered the temperature measured at each sampling site at a depth of 80 cm, expressed as annual mean temperature. The pH values of the fine material varied between 7.7 and 8.1 at the 16 sampling sites. The OM values ranged from 0.05% to 7.85%.

In fungi, none of the diversity measures were influenced by any of the habitat characteristics examined (Table 2). In contrast, species richness and Shannon diversity of vascular plants were affected by annual mean temperature (Table 2). Both species richness and Shannon diversity tended to increase with increasing mean temperature (Table S6). Species richness of vascular plants was also influenced by the pH of the fine material (Table 2). Species richness decreased with increasing fine material pH (Table S6). Furthermore, there was a significant interaction between valley and habitat type on vascular plant species richness (Table 2). This interaction is mainly due to the fact that in Val Sassa the plant species richness was higher on the rock glacier and lower in the lateral scree field than in the corresponding habitats in Valletta (Table 1).

Invertebrate species richness and rarefied species richness were influenced by moss cover (Table 2); both decreased with increasing moss cover (Table S6). Invertebrate abundance was affected by elevation and moss cover (Table 2). The abundance increased with increasing moss cover and showed a U-shaped relationship with elevation (Table S6). Invertebrate evenness was influenced by the pH of the fine material (Table 2), although no clear direction is discernible due to the large variation (Table 1).

When considering arthropods excluding insects, their species richness and rarefied species richness were affected by annual mean temperature and moss cover (Table 2). Both species richness and rarefied species richness decreased with increasing annual mean temperature, while in both cases no direction is apparent in relation to the moss cover due to the large variation (Table S6). Furthermore, species richness was affected by vascular plant cover (Table 2), although no obvious direction of influence is discernible due to the large variation (Table S6). There was also a significant interaction between valley and habitat type on the species richness of this animal group (Table 2). This interaction is mainly due to the fact that in Val Sassa, species richness was higher in the foreland than on the rock glacier, while in Valletta the opposite was the case (Table 1). The abundance of this arthropod group was influenced by both the moss and vascular plant cover (Table 2). The abundance decreased with increasing moss cover, while no clear relationship to the vascular plant cover is visible (Table 3). Evenness of this arthropod group was affected by moss cover and annual mean temperature (Table 2). Evenness tended to increase with increasing moss cover, while no clear direction regarding mean temperature is apparent (Table S6).

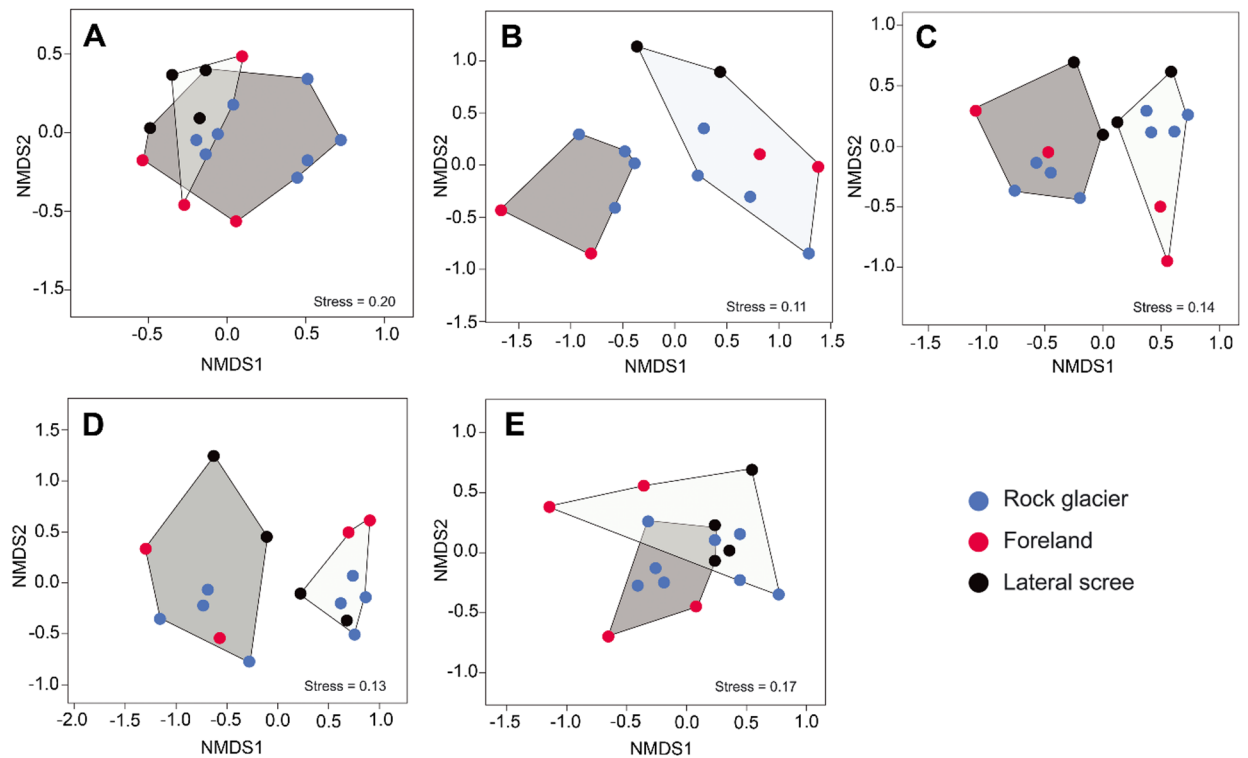
In contrast to the other arthropods, insect species richness was not affected by any of the habitat characteristics studied (Table 2). However, insect abundance was influenced by elevation (Table 2). The abundance decreased with increasing elevation (Table S6). Furthermore, Shannon diversity of insects was influenced by annual mean temperature (Table 2). Insect diversity tended to increase with increasing annual mean temperature (Table S6).

### Effects of habitat characteristics on species composition

PERMANOVAs revealed that the species composition of all organism groups differed between the two valleys and between the three habitat types (Table 3). Interestingly, the elevation of the sampling sites had no effect of

	Fungi		Vascular plants	
	R <sup>2</sup>		R <sup>2</sup>	
Valley	0.162	F <sub>1,15</sub> = 3.81, <b>P = 0.001</b>	0.204	F <sub>1,13</sub> = 4.67, <b>P = 0.001</b>
Habitat	0.200	F <sub>2,15</sub> = 2.34, <b>P = 0.001</b>	0.221	F <sub>2,13</sub> = 2.52, <b>P = 0.002</b>
Elevation	–	–	0.060	F <sub>1,13</sub> = 1.38, <b>P = 0.167</b>
Temperature	0.076	F <sub>1,15</sub> = 1.90, <b>P = 0.035</b>	0.076	F <sub>1,13</sub> = 1.74, <b>P = 0.042</b>
Moss cover	0.078	F <sub>1,15</sub> = 1.91, <b>P = 0.034</b>	0.094	F <sub>1,13</sub> = 2.16, <b>P = 0.002</b>
Vegetation cover	–	–	0.082	F <sub>1,13</sub> = 1.87, <b>P = 0.035</b>
OM	–	–	–	–
pH	0.061	F <sub>1,15</sub> = 1.42, <b>P = 0.154</b>	–	–
Valley x habitat	0.112	F <sub>2,15</sub> = 1.41, <b>P = 0.106</b>	–	–
	<b>All invertebrates</b>		<b>Arthropods excluding insects</b>	<b>Insects</b>
	R <sup>2</sup>		R <sup>2</sup>	R <sup>2</sup>
Valley	0.297	F <sub>1,15</sub> = 7.74, <b>P = 0.001</b>	0.327	F <sub>1,15</sub> = 10.82, <b>P = 0.001</b>
Habitat	0.149	F <sub>2,15</sub> = 1.94, <b>P = 0.041</b>	0.133	F <sub>2,15</sub> = 2.20, <b>P = 0.042</b>
Elevation	–	–	–	F <sub>1,15</sub> = 1.35, <b>P = 0.222</b>
Temperature	0.074	F <sub>1,15</sub> = 1.94, <b>P = 0.081</b>	0.042	F <sub>1,15</sub> = 1.42, <b>P = 0.222</b>
Moss cover	–	–	0.093	F <sub>1,15</sub> = 3.08, <b>P = 0.024</b>
Vegetation cover	0.085	F <sub>1,15</sub> = 2.22, <b>P = 0.032</b>	0.099	F <sub>1,15</sub> = 3.25, <b>P = 0.014</b>
OM	–	–	–	–
pH	0.049	F <sub>1,15</sub> = 1.27, <b>P = 0.270</b>	–	F <sub>1,15</sub> = 1.52, <b>P = 0.151</b>
Valley x habitat	–	–	0.051	F <sub>1,15</sub> = 1.46, <b>P = 0.195</b>
				F <sub>2,15</sub> = 1.51, <b>P = 0.180</b>

**Table 3.** Summary of PERMANOVA analyses testing the effects of valley, habitat type (rock glacier, foreland, lateral scree field), and habitat characteristics on the species composition of fungi, vascular plants and all invertebrates and arthropods excluding insects, as well as insects separately, in the debris layers of three habitats in two neighbouring valleys (Val Sassa and Valletta) in the Eastern Alps, Switzerland. “–” indicates that the variable was excluded from the model due to the step-wise model reduction procedure. Significant *P*-values (*P* < 0.05) are in bold.



**Fig. 5.** Non-metric multidimensional scaling (NMDS) ordination plot based on the Bray-Curtis dissimilarities in species composition between the two valleys Val Sassa (dark grey) and Valletta (light grey) in different taxonomical groups of organisms in the scree layer of rock glaciers (blue dots), in the forelands (red dots) and lateral scree fields (black dots): (A) fungi, (B) vascular plants, (C) all invertebrates, (D) arthropods excluding insects, and (E) insects.

the species composition of the organism groups (Table 3). NMDS illustrates the fungal OTU compositions in the three habitat types and the two valleys (Fig. 5A). The species composition of fungi was also affected by the annual mean temperature and moss cover (Table 3). Regarding vascular plants, the NMDS analysis illustrates the different species compositions in the two neighbouring valleys (Fig. 5B). Species composition of vascular plants was additionally affected by the annual mean temperature and the cover of both moss and vascular plants (Table 3).

NMDS analysis illustrates the different invertebrate species compositions in the two valleys (Fig. 5C). Some dominant species occurred in very different abundances in the two valleys: the diplopod *Pterygophorosoma alticolum* with 3.0% of all invertebrate individuals captured in Val Sassa (S) compared to 45.6% in Valletta (V); the collembolan *Arrhopalites pygmaeus* with 31.1% in S compared to 14.3% in V; the collembolan *Lepidocyrtus violaceus* with 14.6% in S compared to 3.3% in V; the carabid beetle *Nebria breonii* with 5.6% in S compared to 13.0% in V; and the staphylinid beetle *Leptusa areaensis* with 8.0% in S compared to 0.07% in V. The species composition of all invertebrates was also influenced by plant cover (Table 3). Similarly, the species composition of arthropods (excluding insects) was affected by vascular plant cover but also by moss cover (Table 3). NMDS analysis illustrates the different arthropod species compositions in the two valleys (Fig. 5D). Insect species composition differed not only between the two valleys and the three habitat types (Table 3; Fig. 5E), but was also influenced by the annual mean temperature (Table 3).

The cluster analysis of the invertebrate species assemblages at the 16 sampling sites showed that sites were divided into two main clusters (Fig. S1), which corresponded exactly to the two groups in the NMDS analysis (Fig. 5C). While the assignment of the sampling sites to the two valleys was unambiguous, the most similar species communities from the different sampling sites did not in all cases originate from the same habitat type within a valley (Fig S1).

### Functional feeding groups in different habitats

Rock glaciers, forelands and lateral scree fields differed in the percentages of invertebrate individuals from the different functional feeding groups ( $\chi^2 = 95.22$ ,  $df = 6$ ,  $P < 0.0001$ ; Table S7). However, in all three habitat types, decomposers were by far the most frequently represented functional feeding group (rock glaciers 75.3% of all individuals, foreland 72.3%, lateral scree fields 59.1%; Table S7). Predators formed the second most common functional feeding group, but their relative frequencies varied between habitat types, showing the highest frequency in lateral scree fields (27.3% of all individuals; rock glaciers 18.6%, forelands 14.7%; Table S7). Herbivores were found only in very low numbers in the scree layers of rock glaciers and forelands (0.1% each),

while no herbivores were found in lateral scree fields (Table S7). There was no influence of habitat characteristics on the relative frequencies of the different functional groups.

### Indicator species for different habitats

Indicator species analyses allowed the identification of two indicator species for the scree layer of rock glaciers (the staphylinid *Bryaxis judicariensis* ( $P=0.007$ ) and the diplotopod *Orthochordeumella pallida* ( $P=0.018$ )), three for the foreland (the two plant species *Luzula alpinopilosa* ( $P=0.025$ ) and *Juncus jacquini* ( $P=0.025$ ), and the fungal OTU pb608 ( $P=0.012$ )), and five indicator species for the lateral scree fields (the fungal OTUs bp499 ( $P=0.005$ ) and bp505 ( $P=0.034$ ), the spider *Oreonetides glacialis* ( $P=0.037$ ), the staphylinid *Lesteva longoelytrata* ( $P=0.037$ ) and the collembolan *Choreutinula inermis* ( $P=0.020$ )).

### Discussion

Our study shows, to our knowledge for the first time, an impressive hidden biodiversity in the scree layer of active rock glaciers, especially with regard to the species richness of invertebrates living there. Although our study is limited to two rock glaciers and their adjacent habitats, it demonstrates that the scree layer of ice-associated habitats is of considerable importance for the biodiversity in high mountain regions. The habitats investigated in our study are located in a strictly protected area (Swiss National Park) that has not been disturbed by humans for over 110 years<sup>31</sup>. For this reason, human-caused introductions of spores, seeds and invertebrates in recent decades are very unlikely.

In the European Alps, vascular plants have been studied on several rock glaciers of different rock types (e.g. <sup>12,13,23,25,53,54</sup>). The diversity of fungi has received little attention<sup>24</sup>. In two cases, invertebrates active on the debris surface of rock glaciers were examined<sup>13,25</sup>. However, invertebrates living in the scree layer of rock glaciers have not yet been investigated. The scree layer represents a special subterranean habitat in high alpine areas. The surface layer of rock glaciers consists mainly of coarse rock debris. With increasing depth, fine grained material gradually becomes abundant. In the small empty spaces, a special community of invertebrates can exist under conditions that are less extreme than on the surface. Our measurements show that daily temperature fluctuations are dampened in the scree layer and that at 80 cm depth the temperature is significantly higher during winter than in the surface area.

### Fungi

The fungal diversity recorded on rock glaciers (42 OTUs) and in lateral scree fields (44 OTUs) in our study cannot be compared with that of other studies, as these habitats have not yet been investigated. Sannoni et al.<sup>24</sup> examined the fungal community in the permafrost layer of a rock glacier at a depth of 410–520 cm, which does not correspond to the debris layer of our study. However, several studies have examined the fungal communities of glacier forelands in high-alpine regions of Europe and have shown a large range of 7–611 OTUs (e.g. <sup>55–57</sup>). This large variability can be explained by different successional stages of the habitat and/or by differences in study design and soil sampling. This is particularly true when samples were collected at different soil depths (0–10 cm in most studies, 0–80 cm in our study), when different sampling efforts were employed, and when different molecular methods and barcoding regions (ITS1, ITS2) were used for profiling the fungal community. The 45 OTUs found in our study in the glacier forelands lies at the lower end of a wide range of OTUs reported in other studies<sup>55–57</sup>. This suggests that the forelands studied are still in an early stage of succession.

Spores are the main dispersal mode of fungi<sup>58</sup>. The quantity and diversity of fungal spores deposited in a habitat is determined by the regional composition of fungi, local environment conditions including wind exposure and water flow, and the dispersal capacity of specific taxa<sup>58–60</sup>. We found no differences between the two valleys and the three habitat types in the various diversity measures. This can be explained by the similar dispersal abilities of fungi from the same regional species pool. In contrast, the fungal OUT composition differed between valleys and habitat types. This could be due to slight differences in the elevation and exposure of the sampling sites, as well as local microhabitat conditions. For example, differences in water flow in the debris layer of the habitats can cause differences in fungal species composition<sup>58</sup>.

### Vascular plants

Our results on vascular plant diversity can be compared with other studies on rock glaciers, as the same methods were used<sup>13,23,53</sup>. On all rock glaciers studied in the European Alps, the vegetation cover shows significant differences between active and inactive rock glaciers<sup>23,53</sup>. Active rock glaciers with dynamic surfaces are generally characterized by sparse vegetation cover ( $\leq 10\%$ ) of vascular plants<sup>53</sup>. Only a few plant individuals and/or small isolated patches of vascular plants (some herbs, grasses, and shrubs) are found among the coarse debris of the rock glacier surface. In our study, the cover of vascular plants of the two active rock glaciers (2.8% and 7.9%) was similar to those recorded in the uppermost area of the rock glacier Äusseres Hochebenkar (4.5%) in Tyrol, Austria<sup>54</sup> and on the active rock glacier La Foppa 1 (10%) in Upper Valtellina, Italy<sup>23</sup>. On the Val Sassa and Valletta rock glaciers, the plants are regularly grazed by ibex (*Capra ibex*) and chamois (*Rupicapra rupicapra*) (H. Lozza, pers. comm.). In addition to wind-dispersed seeds, grazing animals can bring further seeds to the rock glacier with their feces<sup>61</sup>.

The time since the glacier retreated is the key factor for plant colonization of these areas at high elevations<sup>62,63</sup>. As the glacier retreats over time, the amount of fine detrital material (clay/silt, fine sand, coarse sand and gravel) increases, creating more favourable microclimatic conditions for plant colonization ("safe sites"<sup>64</sup>). Besides the quantity and quality of the substrate, the type of disturbance, the microclimate, water supply, length of the growing season and the duration of snow cover are also factors for the occurrence of vascular plants on the scree layer of rock glaciers<sup>53,63</sup>. Furthermore, ongoing surface deformation can influence the local occurrence of plants<sup>53</sup>. However, surface deformation of the scree layer may affect the vegetation cover in a rather modifying

way<sup>23</sup>. In our study, the vascular vegetation consists of various pioneer species (e.g., *Dryas octopetala*, *Papaver alpinum*, *Saxifraga oppositifolia* and *Sedum atratum*), which is typical for disturbed/unstable alpine habitats, and shows similarities to those of other vegetation studies of active rock glaciers in the European Alps<sup>25,53,62</sup>. The fact that 78% of the plant species recorded in our study have small and wind-dispersed seeds (data not shown) underlines the presence of pioneer vegetation on the active rock glacier studied<sup>65</sup>.

The differences in plant diversity and species composition between the two valleys observed in our study can be explained by specific plant traits and other factors<sup>65</sup>. In Val Sassa, a significant proportion of plant species have animal-dispersed seeds (19.2%), but none in Valletta (data not shown). This could be due to different grazing intensity by ibex and chamois in the two valleys. At the sampling sites on the Val Sassa rock glacier, the ice cover retreated many years earlier than at those on the Valletta rock glacier. Thus, plants had more time to colonize the scree layer of the Val Sassa rock glacier than the scree layer of the Valletta rock glacier. Furthermore, the Valletta rock glacier lies at a higher elevation, resulting in a lower average temperature and a shorter growing season.

The lateral scree fields exhibit pronounced debris movement. New rock fragments fall from the cliff faces, and there are few patches of fine material. This makes the establishment of vascular plants difficult in this unstable habitat.

## Invertebrates

Compared to rock glaciers, the glacier foreland is a well-studied habitat in high-alpine regions. Shortly after the ice has melted, bacteria, algae, lichens, and mosses colonize the exposed scree and rock surfaces, enrich them with organic matter, and thus pave the way for vascular plants<sup>66</sup>. The succession at a particular site over time following glacier retreat can be recorded following the sequence of dated study plots in the foreland, known as a chronosequence<sup>66</sup>. Several invertebrate groups including springtails (Collembola), mites (Acari), beetles (Coleoptera), spiders (Araneae) and harvestmen (Opiliones) can be found on barren, vegetation-free soils near the glacier margin<sup>67</sup>. Since there is no organic layer, these pioneer invertebrates are surface-active, but can find shelter in crevices between stones, gravel, and sand grains. The first colonizers are mainly predators<sup>67</sup> and generalist and decomposer springtails<sup>68</sup>. Herbivore and decomposer macroarthropods appear later<sup>69</sup>, but different species assemblages can form<sup>68</sup>.

The invertebrate communities of debris-covered glaciers represent one of the most species-rich continental glaciated environments<sup>70</sup>. This habitat appears to serve as a refuge for cold-adapted ground beetles and spiders<sup>25,26</sup>, springtails known as “glacier fleas”<sup>71</sup>, as well as for nematodes and rotifers<sup>72</sup>. In contrast to debris-covered glaciers, there are few studies on invertebrate communities on rock glaciers. These studies used pitfall traps to capture surface-active individuals<sup>13,25</sup>. As an exception, Gobbi et al.<sup>13</sup> also used two SSDs in which a total of three ground beetle individuals were captured. We focused on invertebrate communities living in the superficial subterranean environment, on previously unknown communities in the scree layer of rock glaciers, forefields, and scree slopes. We used SSDs to capture invertebrates living in the scree layer in a depth of 50–90 cm. A methodological study showed that standard SSDs (1 m long tubes) do indeed capture individuals of invertebrate species naturally active in the scree layer at depths of up to 90 cm, either permanently or during seasonal vertical migrations<sup>73</sup>. Individuals of species that are primarily active at the surface do not appear to follow the tubes to reach the deeper SSDs. This means that our results are only partially comparable with previous studies on surface-active invertebrates on rock glaciers.

We found a higher invertebrate species richness in Val Sassa than in Valletta, but the two valleys did not differ in invertebrate abundance. Differences in species richness can be explained by the different duration of previous glacial ice cover<sup>22</sup>, and the different elevations of the two rock glaciers studied. Since the two rock glaciers differ in duration of previous glacial ice cover and elevation, a significant valley effect resulted. Interestingly, the three habitat types did not differ in either invertebrate diversity or abundance. This is surprising because the lateral scree fields hardly contained any vascular plants. However, the scree fields consist of coarser material, which forms larger voids that in turn allow for higher activity of the invertebrates. In contrast, the presence of mosses appears to have a negative impact on the occurrence of some invertebrate species, as species abundance decreased with increasing moss cover. This could be explained by the dominance of a few species under dense moss cover. However, if we consider arthropods without insects, species richness was influenced by the annual average temperature and moss cover. Surprisingly, species richness decreased with increasing annual average temperature, suggesting an increasing number of cold-adapted species at sampling sites with low annual temperatures. This is in accordance with other studies on arthropods in colluvial MSS in Spain and Portugal<sup>74,75</sup>. The group “arthropods excluding insects” included many millipede species, some of them with numerous individuals. The species richness and abundance of these decomposers could be related to moss cover. In contrast to the other arthropods, insect species richness was not affected by any of the habitat characteristics studied. However, insect abundance decreased with increasing elevation.

The species composition of all invertebrates differed between the two valleys and between the three habitat types. The Valletta rock glacier is located at a higher elevation than the Val Sassa rock glacier, and the ice glacier covering it disappeared later than the one in Val Sassa. The species composition of invertebrates on the Valletta rock glacier therefore reflects an earlier stage of colonization. This species composition also contains more cold-adapted species than that in Val Sassa. Only 12 invertebrate species were found exclusively in Valletta, but these include several high-mountain specialists such as *Oreonetides glacialis*, *Leistus montanus rhaeticus*, *Nebria castanea* or *Stenus glacialis*.

The results of the cluster analysis of the invertebrate species assemblages at the 16 sampling sites showed that the assignment of the sampling points to the two valleys was unambiguous and thus confirmed the difference in species composition between the two valleys. Interestingly, in some cases the most similar species assemblages did not originate from the same habitat type within a valley (Fig. S1). In these cases, not only the habitat type but also the elevation seems to have an influence on the species composition.

The three habitats studied each exhibited only a minor unique species composition. In general, large overlaps were found between the habitats in terms of species composition. This is reflected in the rather small number of indicator species identified for each habitat type. For the scree layer of rock glaciers the indicator species analysis revealed two indicator species: the staphylinid *Bryaxis judicariensis* and the diplopod *Orthochordeumella pallida*. *Bryaxis judicariensis* is a relatively rare alpine species, but occurs in several regions of the Alps<sup>76</sup>. *Orthochordeumella pallida* is a common mountain and subalpine species found in various habitats in the Swiss National Park<sup>5,77</sup>, but also in lowland forests in Western Europe<sup>78</sup>.

We found two troglobiont (i.e. cave-adapted) species in all three habitat types: the spider *Porrhomma rosenhaueri*<sup>79</sup> and the dipluran *Plusiocampa caprai*<sup>80</sup>, but also several troglophile species (facultative cave species). One staphylinid species discovered in the foreland of Valletta rock glacier was previously unknown to science (*Leptusa* new species; A. Szallies, in prep.). With a few exceptions, the captured individuals of Diptera and other groups have not yet been identified to their species, and are therefore not considered in this study. However, among the braconid wasps, *Aspilota umbrosa* was found in the scree layer of the Val Sassa rock glacier, marking the second record worldwide and the first in Europe<sup>81</sup>. Since the subterranean invertebrate community in the scree layer of rock glaciers has hardly been studied to date, further new and extremely rare species are likely to be discovered in the future.

Decomposer followed by predators constituted the most common functional feeding groups in all three habitat types. This reflects a trophic structure typical of cold, nutrient-poor environments, in which detritus consisting of aeroplankton accumulates, including flying insects that land on snow and scree, thus becoming food for predators and decomposers<sup>11,82</sup>. Thus, the communities found in the three habitat types depend on a constant influx of aeroplankton<sup>82</sup>. Characteristics of the three habitats do not appear to influence the relative frequencies of the different functional groups.

### Climate refugia

The scree cover of rock glaciers insulates their interior from outside air currents and promotes internal thermal regimes that support ice accumulation and retention<sup>15</sup>. For this insulation, rock glaciers are expected to respond to climate warming more slowly than pure glaciers. This in turn led to the idea that rock glaciers can serve as climate refugia for many plant and animal species in the short term<sup>15,25</sup>. However, under continued warming, rock glaciers will lose their permanent ice<sup>15,22</sup>. Finally, only scree fields remain. Therefore, it is uncertain whether rock glaciers can function as climate refugia in the long term. The drastic change in this habitat particularly affects cold-adapted invertebrates<sup>11</sup>.

### Conclusions

The biodiversity of rock glaciers has been overlooked in ecological studies, even though rock glaciers are common in mountain ranges. Many aspects of rock glacier biodiversity are still unknown. Our study shows that the scree layer of rock glaciers is inhabited by a considerable diversity of organisms. Furthermore, other, previously unknown species are likely to be present there. Our study also shows that the scree layer of rock glaciers exhibits a certain unique species composition. However, this also applies to the glacier foreland and the lateral scree field. Together, the three habitats provide a basis for a diverse high-alpine biodiversity. Due to global warming, rock glaciers are a highly threatened habitat. In the European Alps, many of them will no longer exist in a few decades<sup>22</sup>. Rock glaciers alone will hardly be able to function as climate refugia for cold-adapted species in this mountain region in the long term. However, together with scree slopes and other landforms with cool microhabitats at higher elevations, they could preserve some species.

### Data availability

Data are available in the Supplementary material: Table S1–Table S5.

Received: 12 January 2026; Accepted: 20 March 2026

Published online: 25 March 2026

### References

- Rahbek, C. et al. Humboldt's enigma: What causes global patterns of mountain biodiversity? *Science* **365**, 1108–1113 (2019).
- Muhlfeld, C. C. et al. Specialized meltwater biodiversity persists despite widespread deglaciation. *PNAS* **117**, 12208–12214 (2020).
- Baur, B. & Baur, A. Snails keep the pace: Shift in upper elevational limit on mountain slopes as a response to climate warming. *Can. J. Zool.* **91**, 596–599 (2013).
- Auffret, A. G. & Svenning, J. C. Climate warming has compounded plant responses to habitat conversion in northern Europe. *Nat. Commun.* **13**, 7818 (2022).
- Gilgado, J. D., Rusterholz, H. P. & Baur, B. Millipedes step up: Species extend their upper elevational limit in the Alps in response to climate warming. *Insect Conserv. Divers.* **15**, 61–72 (2022).
- La Sorte, F. A. & Jetz, W. Projected range contractions of montane biodiversity under global warming. *Proc. R. Soc. B.* **277**, 3401–3410 (2010).
- Noetzli, J. et al. Enhanced warming of European mountain permafrost in the early 21st century. *Nat. Commun.* **15**, 10508 (2024).
- Klein, G., Vitasse, Y., Rixen, C., Marty, C. & Rebetez, M. Shorter snow cover duration since 1970 in the Swiss Alps due to earlier snowmelt more than to later snow onset. *Clim. Change*. **139**, 637–649 (2016).
- Beniston, M. et al. The European mountain cryosphere: A review of its current state, trends, and future challenges. *Cryosphere* **12**, 759–794 (2018).
- Kenner, R., Noetzli, J., Bazargan, M. & Scherrer, S. C. Response of alpine ground temperatures to a rising atmospheric 0 °C isotherm in the period 1955–2021. *Sci. Total Environ.* **924**, 171446 (2024).
- Hock, R. et al. High mountain areas. *Intergovern. Panel Clim. Change (IPCC)*. **2**, 1–94 (2019).
- Piccinelli, S. & Cannone, N. Divergent responses of alpine rock glaciers to climate change: A review of ecological and abiotic dynamics. *Permafrost. Periglac. Process.* **36**, 438–450 (2025).

13. Ashcroft, M. B. Identifying refugia from climate change. *J. Biogeogr.* **37**, 1407–1413 (2010).
14. Gobbi, M. et al. Physical and biological features of an active rock glacier in the Italian Alps. *Holocene* **24**, 1624–1631 (2014).
15. Millar, C. I. et al. Potential climatic refugia in semi-arid, temperate mountains: Plant and arthropod assemblages associated with rock glaciers, talus slopes, and their forefield wetlands, Sierra Nevada, California, USA. *Quaternary Intern.* **387**, 106–121 (2015).
16. Brighenti, S. et al. Rock glaciers and related cold rocky landforms: overlooked climate refugia for mountain biodiversity. *Global Change Biol.* **27**, 1504–1517 (2021).
17. Reinosch, E. et al. Rock glacier inventory of the western Nyainqêntanglha Range, Tibetan Plateau, supported by InSAR time series and automated classification. *Permafrost. Periglac. Processes.* **32**, 1–16 (2021).
18. Kellerer-Pirklbauer, A. et al. Acceleration and interannual variability of creep rates in mountain permafrost landforms (rock glacier velocities) in the European Alps in 1995–2022. *Environ. Res. Lett.* **19**, 034022 (2024).
19. Haeberli, W. et al. Permafrost creep and rock glacier dynamics. *Permafrost. Periglac. Processes.* **17**, 189–214 (2006).
20. Haeberli, W. & Burn, C. R. *Natural Hazards in Forests: Glacier and Permafrost Effects as Related to Climate Change* (CABI, 2002).
21. Anderson, R. S., Anderson, L. S., Armstrong, W. H., Rossi, M. W. & Crump, S. E. Glaciation of alpine valleys: The glacier–debris-covered glacier–rock glacier continuum. *Geomorphology* **311**, 127–142 (2018).
22. Machado, A. M. T. et al. 100 years of monitoring in the Swiss National Park reveals overall decreasing rock glacier velocities. *Nat Commun. Earth Environ.* **5** (138) (2024).
23. Cannone, N. & Gerdol, R. Vegetation as an ecological indicator of surface instability in rock glaciers. *Arct. Antarct. Alp. Res.* **35**, 384–390 (2003).
24. Sannino, C. et al. Abiotic factors affecting the bacterial and fungal diversity of permafrost in a rock glacier in the Stelvio Pass (Italian Central Alps). *Appl. Soil. Ecol.* **166**, 104079 (2021).
25. Tampucci, D. et al. Ecology of active rock glaciers and surrounding landforms: Climate, soil. *Plants Arthropods Boreas* **46**, 185–198 (2017).
26. Gobbi, M., Isaia, M. & De Bernardi, F. Arthropod colonisation of a debris-covered glacier. *Holocene* **21**, 343–349 (2011).
27. Gobbi, M. et al. Life in harsh environments: Carabid and spider trait types and functional diversity on a debris-covered glacier and along its foreland. *Ecol. Entomol.* **42**, 838–848 (2017).
28. Tampucci, D. et al. Debris-covered glaciers as habitat for plant and arthropod species: Environmental framework and colonization patterns. *Ecol. Complex.* **32**, 42–52 (2017).
29. Mammola, S. et al. Ecology and sampling techniques of an understudied subterranean habitat: The Milieu Souterrain Superficiel (MSS). *Sci. Nat.* **103**, 1–24 (2016).
30. IUCN/WCMC. *Guidelines for Protected Area Management Categories* (IUCN, 1994).
31. Baur, B. & Scheurer, T. (eds) *Wissen schaffen – 100 Jahre Forschung im Schweizerischen Nationalpark. Nationalpark-Forschung in der Schweiz 100/I* (Haupt, 2013).
32. Trümpy, R., Schmid, S., Conti, P. & Froitzheim, N. Erläuterungen zur geologischen Karte 1:50'000 des Schweizerischen Nationalparks. *Nationalpark Forsch. Schweiz.* **87**, 1–40 (1997).
33. Barsch, D. *Rock Glaciers* (Springer, 1996).
34. Janke, J. R., Regmi, N. R., Giardino, J. R. & Vitek, J. D. Rock glacier. In *Treatise on Geomorphology. Glacial and Periglacial Geomorphology* (eds Shroder, J., Giardino, B. & Harbor, J.). Vol. 8. 238–273 (Academic Press, 2013).
35. Meisch, M., Wipf, A., Denneler, B., Battaglia, J. & Benz, B. *Die Gletscher der Schweizer Alpen: Gletscherhochstand 1850. Aktuelle Vergletscherung, Gletscherschwundsenarien. Schlussbericht NFP 31*. 2nd Ed. (vdf, 2000).
36. Clasen, L. A., Detheridge, A. P., Scullion, J. & Griffith, G. W. Soil stabilisation for DNA metabarcoding of plants and fungi. Implications for sampling at remote locations or via third-parties. *Metabarcod Metagenom.* **4**, 135–147 (2020).
37. White, T. J., Bruns, T. D., Lee, S. & Taylor, J. W. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In *PCR Protocols: A Guide to Methods and Applications*. (eds Gelfand, M. A., Sninsky, D. H. et al.). 315–322 (Academic Press, 1990).
38. Ranjard, L. et al. Characterization of bacterial and fungal soil communities by automated ribosomal intergenic spacer analysis fingerprints: Biological and methodological variability. *Appl. Environ. Microbiol.* **671**, 4479–4487 (2001).
39. Taggart, J. M., Cahill, J. F., Jr, McNickle, G. G. & Hall, J. C. Molecular identification of roots from a grassland community using size differences in fluorescently labelled PCR amplicons of three cpDNA regions. *Mol. Ecol. Resour.* **1**, 185–195 (2011).
40. Li, F., Hullar, M. A. J. & Lampe, J. W. Optimization of terminal restriction fragment polymorphism (TRFLP) analysis of human gut microbiota. *J. Microbiol. Meth.* **68**, 303–311 (2007).
41. Barto, E. K. et al. Differences in arbuscular mycorrhizal fungal communities associated with sugar maple seedlings in and outside of invaded garlic mustard forest patches. *Biol. Invasions.* **13**, 2755–2762 (2011).
42. Mueller-Dombois, D. & Ellenberg, H. *Aims and Methods of Vegetation Ecology* (Blackburn, 2002).
43. Lauber, K., Wagner, G. & Gygas, A. *Flora Helvetica*. 5th Ed. (Haupt, 2012).
44. Brock, B. W. et al. Meteorology and surface energy fluxes in the 2005–2007 ablation seasons at the Miage debris-covered glacier, Mont Blanc Massif, Italian Alps. *J. Geophys. Res. Atmos.* **115**, D09106 (2010).
45. Allen, S. E. *Chemical Analysis of Ecological Materials*. 2nd Ed. (Blackwell, 1989).
46. R Core Team. *R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing.* <https://www.R-project.org/> (2025).
47. Hsieh, T. C., Ma, K. H. & Chao, A. iNEXT: An R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods Ecol. Evol.* **7**, 1451–1456 (2016).
48. Oksanen, J. et al. R Package Version 3.6.3. *Vegan Community Package* (2019).
49. Wagenmakers, E. J. & Farrell, S. AIC model selection using akaike weights. *Psychonomic Bull. Rev.* **11**, 192–196 (2004).
50. Anderson, M. J. *PERMANOVA: A FORTRAN Computer Program for Permutational Multivariate Analysis of Variance* (University of Auckland, 2005).
51. Borcard, D., Gillet, F. & Legendre, P. *Numerical Ecology in R* (Springer, 2011).
52. De Cáceres, M. & Legendre, P. Associations between species and groups of sites: Indices and statistical inference. *Ecology* **90**, 3566–3574 (2009).
53. Burga, C. A., Frauenfelder, R., Ruffet, J., Hoelzle, M. & Käab, A. Vegetation on alpine rock glacier surfaces: A contribution to abundance and dynamics on extreme plant habitats. *Flora* **199**, 505–515 (2004).
54. Grassmair, R. & Erschbamer, B. Die Besiedelung des Blockgletschers Äusseres Hochebenkar im Vergleich zur angrenzenden Vegetation. In *Forschung am Blockgletscher – Methoden und Ergebnisse* (eds Erschbamer, B. & Schallhart, N.). 159–180 (Innsbruck University Press, 2015).
55. Zumsteg, A. et al. Bacterial, archaeal and fungal succession in the forefield of a receding glacier. *Microbiol. Ecol.* **63**, 552–564 (2012).
56. Brown, S. P. & Jumpponen, A. Contrasting primary successional trajectories of fungi and bacteria in retreating glacier soils. *Mol. Ecol.* **23**, 481–497 (2014).
57. Tian, J. et al. Ecological succession pattern of fungal community in soil along a retreating glacier. *Front. Microbiol.* **8** (2017).
58. Chaudhary, V. B., Aguilar-Trigueros, C. A., Mansour, I. & Rillig, M. C. Fungal dispersal across spatial scales. *Annu. Rev. Ecol. Evol. Syst.* **53**, 69–85 (2022).
59. Edman, M., Gustafsson, M., Stenlid, J., Jonsson, B. & Ericson, L. Spore deposition of wood-decaying fungi: Importance of landscape composition. *Ecography* **27**, 103–111 (2004).

60. Norros, V. et al. Do small spores disperse further than large spores? *Ecology* **95**, 1612–1621 (2014).
61. Nathan, R. & Muller-Landau, H. C. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends Ecol. Evol.* **7**, 278–285 (2000).
62. Burga, C. A. et al. Plant succession and soil development on the foreland of the Morteratsch glacier (Pontresina, Switzerland). Straight forward or chaotic? *Flora* **205**, 561–576 (2010).
63. Schuhmann, K., Gewolf, S. & Tackenberg, O. Factors affecting primary succession of glacier foreland vegetation in the European Alps. *Alp. Bot.* **126**, 105–117 (2016).
64. Erschbamer, B., Niederfringer-Schlag, R. & Winkler, E. Colonization pattern on a central Alpine glacier foreland. *J. Veg. Sci.* **19**, 855–862 (2008).
65. Erschbamer, B. & Mayer, R. Can successional species groups be discriminated on their life history traits? A study from a glacier foreland in the Central Alps. *Plant. Ecol. Divers.* **4**, 341–351 (2011).
66. Hågvar, S. IntechOpen, Primary succession in glacier forelands: How small animals conquer new land around melting glaciers. In *International Perspectives on Global Environmental Change* (eds. Young, S. S. & Silvern, S. E.). 151–172 (2012).
67. Kaufmann, R. Invertebrate succession on an alpine glacier foreland. *Ecology* **82**, 2261–2278 (2001).
68. Hågvar, S. et al. Ecosystem birth near melting glaciers: A review on the pioneer role of ground-dwelling arthropods. *Insects* **11**, 1–35 (2020).
69. Gobbi, M., De Bernardi, F., Pelfini, M., Rossaro, B. & Brandmayr, P. Epigeal arthropod succession along a 154-year glacier foreland chronosequence in the Forni valley (Central Italian Alps). *Arct. Antarct. Alp. Res.* **38**, 357–362 (2006).
70. Nakawo, M., Raymond, C. F. & Fountain, A. *Debris-Covered Glaciers*. Publication No. 264 (IAHS Press, 2000).
71. Valle, B. et al. The unexplored biodiversity of ‘glacier fleas’ (Hexapoda: Collembola): Taxonomy, distribution and ecology in the European Alps and Apennines. *J. Zool. Syst. Evol. Res.* **1616350** (2025).
72. Azzoni, R. S., Franzetti, A., Fontaneto, D., Zullini, A. & Ambrosini, R. Nematodes and rotifers on two alpine debris-covered glaciers. *Italian J. Zool.* **82**, 616–623 (2015).
73. Gilgado, J. D., Rusterholz, H. P. & Baur, B. Checking the depth specificity of a subterranean sampling device in alpine rock debris. *Subterr. Biol.* **52**, 135–142 (2025).
74. Ledesma, E. et al. Arthropod biodiversity patterns point to the Mesovoid Shallow Substratum (MSS) as a climate refugium. *Zoology* **141**, 125771 (2020).
75. Eusebio, R. P. et al. Temporal and spatial dynamics of arthropod groups in terrestrial subsurface habitats in Central Portugal. *Zoology* **147**, 125931.
76. Käfer, E. Lompe, A. (Ed.). <https://www.coleonet.de/coleo/index.htm>. Accessed 1 Aug 2025 (2025).
77. Gilgado, J. D. et al. Six groups of ground-dwelling arthropods show different diversity responses along elevational gradients in the Swiss Alps. *PLoS ONE*. **17** (7), e0271831 (2022).
78. Kime, R. D. & Enghoff, H. Atlas of European millipedes 3: Order Chordeumatida (class Diplopoda). *Eur. J. Taxonomy*. **769**, 1–244 (2021).
79. Mammola, S. et al. A trait database and updated checklist for European subterranean spiders. *Sci. Data*. **9** (236), 1–13 (2022).
80. Christian, E., Graf, W. & Moog, O. *Plusiocampa caprai* – Ein Höhlentier in den Kärntner Zentralalpen. *Carinthia II*. **186/106**, 387–392 (1996).
81. Peris-Felipo, F. J., Gilgado, J. D., Belokobylskij, S. A. & Baur, B. From a volcanic area on the Kamchatka Peninsula (Northeast Asia) to a rock glacier in the Swiss Alps: A new record of *Aspilota umbrosa* Belokobylskij, 2007 (Hymenoptera, Braconidae). *Rev. Suisse Zool.* **131**, 121–130 (2024).
82. Crosta, A. et al. Ecological interactions in glacier environments: A review of studies on a model Alpine glacier. *Biol. Rev.* **100**, 227–244 (2025).

## Acknowledgements

We thank the Swiss National Park for granting permission and logistical support for fieldwork. We are grateful to S. Wipf, C. Rossi, S. Wiesmann, S. Campell Andri and S. Bunte (staff members of SNP) for advice and help during fieldwork and the staff of the Chamanna Cluozza for accommodation. We are thankful to A. Criado, I. Gilgado, L. Yapura, N. Meier, S. Fröhlicher, J. Muñoz-Santiago, U. Vogel and S. Meyer for assistance in the field, the specialists (listed in the text) for species identifications and U. Rehsteiner and S. Liersch (Bündner Naturmuseum Chur) for their help in preparing the specimens for the collection, and A. Jiménez-Valverde and two anonymous reviewers for comments on the manuscript.

## Author contributions

BB and JDG thought up the initial idea and approach. JDG and HPR conducted the field surveys and sampling. JDG sorted the invertebrates and identified them with help of experts. HPR undertook the molecular analyses and analysed the data. BB sought financial support for the project and wrote the initial draft. All the authors contributed to the final draft.

## Funding

Funding was obtained from the SNP Research Commission, the University of Basel and the ‘Stiftung Sammlung Naturmuseum Chur’.

## Declarations

## Competing interests

The authors declare no competing interests.

## Additional information

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1038/s41598-026-45647-2>.

**Correspondence** and requests for materials should be addressed to J.D.G.

**Reprints and permissions information** is available at [www.nature.com/reprints](http://www.nature.com/reprints).

**Publisher's note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

**Open Access** This article is licensed under a Creative Commons Attribution-NonCommercial-NoDerivatives 4.0 International License, which permits any non-commercial use, sharing, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if you modified the licensed material. You do not have permission under this licence to share adapted material derived from this article or parts of it. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by-nc-nd/4.0/>.

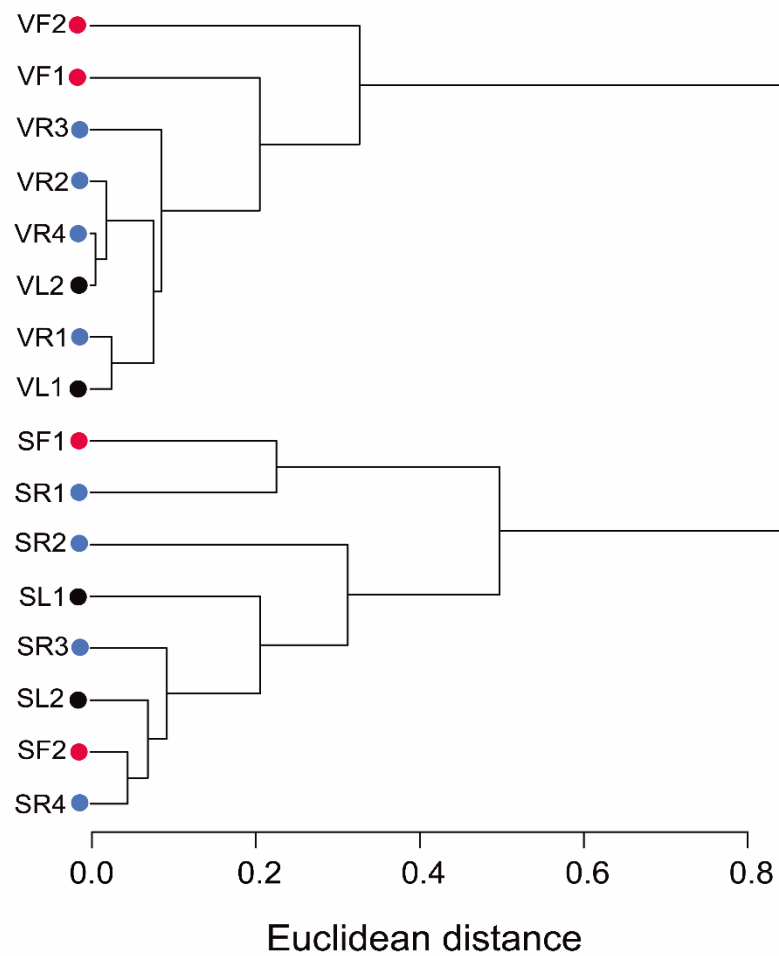
© The Author(s) 2026

## **Supplementary information**

### **Unexpected high subterranean biodiversity on rock glaciers threatened by global warming**

José D. Gilgado, Hans-Peter Rusterholz & Bruno Baur

**Fig. S 1.** Dendrogram of hierarchical cluster analysis for the similarities of invertebrate communities trapped with SSDs in the scree layer of rock glaciers (R, blue dots), glacier forelands (F, red dots), and lateral scree fields (S, black dots) in two neighbouring valleys (S = Val Sassa and V = Valletta) in the Eastern Alps, Switzerland. The dendrogram was calculated using the Ward method and is based on the Euclidean distance as the similarity index.



**Table S1.** Coordinates and characteristics of the sampling sites in the three habitats (rock glacier, foreland, lateral scree) in two neighbouring valleys (Val Sassa and Vailletta) in the Eastern Alps, Switzerland.

Valley	Habitat	Site code	Coordinates	Elevation (m a.s.l)	Temperature <sup>1</sup> (°C)	Vascular plant cover (%)	Moss cover (%)	pH <sup>2</sup>	OM <sup>3</sup> (%)
Val Sassa	Rock glacier	SR1	46°37'59.53"N/10°06'53.31"E	2117	0.73	11.7	2.5	8.08	3.63
	Rock glacier	SR2	46°37'50.79"N/10°06'48.05"E	2190	2.20	11.6	1.3	8.83	5.96
	Rock glacier	SR3	46°37'44.07"N/10°06'43.60"E	2235	0.79	2.9	0.7	8.6	1.35
	Rock glacier	SR4	46°37'35.09"N/10°06'38.93"E	2306	1.22	5.3	0.3	8.51	1.09
	Foreland	SF1	46°38'02.55"N/10°06'56.21"E	2100	0.79	46.0	0	7.66	7.85
	Foreland	SF2	46°38'01.65"N/10°06'54.34"E	2096	-1.64	4.9	7.5	8.28	1.49
	Lateral scree	SL1	46°37'39.72"N/10°06'44.66"E	2280	0.70	0	0	9.04	0.46
	Lateral scree	SL2	46°37'49.88"N/10°06'50.25"E	2198	-0.96	0	0	8.80	0.64
Vailletta	Rock glacier	VR1	46°38'27.20"N/10°06'9.95"E	2533	-0.79	2.3	1.0	9.00	1.90
	Rock glacier	VR2	46°38'19.01"N/10°06'3.44"E	2590	0.85	2.3	0	8.79	0.36
	Rock glacier	VR3	46°38'10.23"N/10°05'59.25"E	2645	1.39	4	0	8.99	0.71
	Rock glacier	VR4	46°38'30.09"N/10°05'52.33"E	2693	1.15	2.3	0.2	8.66	4.12
	Foreland	VF1	46°38'30.93"N/10°06'11.03"E	2494	1.86	8.7	2.8	8.54	0.79
	Foreland	VF2	46°38'29.54"N/10°06'10.42"E	2505	1.66	8.3	2.7	8.24	2.91
	Lateral scree	VL1	46°38'19.33"N/10°06'0.17"E	2600	-0.76	0.25	0	9.09	0.55
	Lateral scree	VL2	46°38'14.39"N/10°05'49.64"E	2702	1.05	1.0	0	8.61	0.05

<sup>1</sup> Average air temperature at 80 cm depth over 1 year

<sup>2</sup> pH of the fine material of the debris layer

<sup>3</sup> Organic matter content of the fine material of the debris layer

**Table S2.** Dates of the installation of the SSDs and sampling schedule.

Valley	Habitat	Code	Installation date	Sampling date 1		Sampling date 2		Sampling date 3		Sampling date 4		Sampling date 5		Sampling date 6		Sampling date 7	
				Sample no.	Trap recovery date	Sample no.	Trap recovery date	Sample no.	Trap recovery date	Sample no.	Trap recovery date	Sample no.	Trap recovery date	Sample no.	Trap recovery date	Sample no.	Trap recovery date
Val Sassa	Foreland	SF1	25/07/2019	1	25/09/2019	8	28/07/2020	16	23/09/2020	32	14/07/2021	48	15/09/2021	64	21/06/2022	80	07/09/2022
Val Sassa	Foreland	SF2	25/07/2019	2	25/09/2019	9	28/07/2020	17	23/09/2020	33	14/07/2021	49	15/09/2021	65	21/06/2022	81	07/09/2022
Val Sassa	Rock glacier	SR1	25/07/2019	3	25/09/2019	10	28/07/2020	18	23/09/2020	34	14/07/2021	50	15/09/2021	66	21/06/2022	82	07/09/2022
Val Sassa	Rock glacier	SR2	25/07/2019	4	25/09/2019	11	28/07/2020	19	23/09/2020	35	14/07/2021	51	15/09/2021	67	21/06/2022	83	07/09/2022
Val Sassa	Rock glacier	SR3	24/07/2019	5	25/09/2019	12	28/07/2020	20	23/09/2020	36	14/07/2021	52	15/09/2021	68	21/06/2022	84	07/09/2022
Val Sassa	Rock glacier	SR4	24/07/2019	6	25/09/2019	13	28/07/2020	21	23/09/2020	37	14/07/2021	53	15/09/2021	69	21/06/2022	85	07/09/2022
Val Sassa	Lateral scree	SL1	26/09/2019	–	–	14	28/07/2020	22	23/09/2020	38	14/07/2021	54	15/09/2021	70	21/06/2022	86	07/09/2022
Val Sassa	Lateral scree	SL2	24/07/2019	7	25/09/2019	15	28/07/2020	23	23/09/2020	39	14/07/2021	55	15/09/2021	71	21/06/2022	87	07/09/2022
Valletta	Foreland	VF1	20/08/2020	–	–	–	–	24	22/09/2020	40	13/07/2021	56	14/09/2021	72	22/06/2022	88	06/09/2022
Valletta	Foreland	VF2	20/08/2020	–	–	–	–	25	22/09/2020	41	13/07/2021	57	14/09/2021	73	22/06/2022	89	06/09/2022
Valletta	Rock glacier	VR1	20/08/2020	–	–	–	–	26	22/09/2020	42	13/07/2021	58	14/09/2021	74	22/06/2022	90	06/09/2022
Valletta	Rock glacier	VR2	06/08/2020	–	–	–	–	27	22/09/2020	43	15/07/2021	59	14/09/2021	75	22/06/2022	91	06/09/2022
Valletta	Rock glacier	VR3	06/08/2020	–	–	–	–	28	22/09/2020	44	15/07/2021	60	14/09/2021	76	22/06/2022	92	06/09/2022
Valletta	Rock glacier	VR4	05/08/2020	–	–	–	–	29	22/09/2020	45	15/07/2021	61	14/09/2021	77	22/06/2022	93	06/09/2022
Valletta	Lateral scree	VL1	06/08/2020	–	–	–	–	30	22/09/2020	46	15/07/2021	62	14/09/2021	78	22/06/2022	94	06/09/2022
Valletta	Lateral scree	VL2	05/08/2020	–	–	–	–	31	22/09/2020	47	15/07/2021	63	14/09/2021	79	22/06/2022	95	06/09/2022

**Table S3.** Abundance of invertebrates in the debris layers of three habitats (rock glacier, foreland, lateral scree field) in two neighbouring valleys (Val Sassa and Valletta) in the Eastern Alps, Switzerland. Abundance indicates the total number of individuals captured during the entire study period. The functional feeding group of each species is also presented. We only present references for groups with trophic variability: harvestmen, diplurans, springtails, and rove beetles. All spiders, pseudoscorpions, centipedes, and ground beetles are Predators, while all snails and millipedes are Decomposers. For several species, there was no available information. In some of these cases, it was inferred from closely related species.

Group	Species	Val Sassa			Valletta			Functional feeding group	Reference
		Rock glacier	Foreland	Lateral scree	Rock glacier	Foreland	Lateral scree		
<b>Gastropoda</b>	<i>Eucobresia glacialis</i>	5	1	0	4	4	0	Decomposer	
	<i>Pyramidula pusilla</i>	0	0	2	0	1	0	Decomposer	
<b>Araneae</b>	<i>Anguliphantes monticola</i>	45	1	3	0	1	0	Predator	
	<i>Asthenargus</i> cf. <i>bracianus</i>	1	0	0	0	0	0	Predator	
	cf. <i>Drassodes</i> sp.	0	2	5	0	0	0	Predator	
	<i>Iberina montana</i>	0	1	0	0	0	0	Predator	
	<i>Lepthyphantes notabilis</i>	2	2	19	0	0	0	Predator	
	<i>Mansuphantes fragilis</i>	0	4	0	0	0	0	Predator	
	<i>Mughiphantes variabilis</i>	1	1	0	3	0	5	Predator	
	<i>Oreonetides glacialis</i>	0	0	0	0	0	3	Predator	
	<i>Pardosa</i> sp.	0	0	1	0	0	0	Predator	
	<i>Porrhomma rosenhaueri</i>	9	18	2	1	0	8	Predator	
	<i>Robertus arundineti</i>	1	0	0	0	0	0	Predator	
	<i>Theridion petraeum</i>	0	2	0	0	0	0	Predator	
	<i>Troglohyphantes sciakyi</i>	0	0	5	0	0	0	Predator	

<b>Opiliones</b>	<i>Walckenaeria capito</i>	17	4	1	2	0	0	Predator	
	<i>Dicranopalpus gasteinensis</i>	0	1	51	7	0	34	Generalist	[1]
	<i>Ischyropsalis dentipalpis</i>	13	2	33	0	0	2	Predator	[2,3]
<b>Pseudoscorpionida</b>	<i>Chthonius tenuis</i>	0	2	0	0	0	0	Predator	
	<i>Neobisium jugorum</i>	33	7	8	10	35	21	Predator	
<b>Chilopoda</b>	<i>Geophilus impressus</i>	1	0	0	0	0	0	Predator	
	<i>Lithobius glacialis</i>	0	3	0	0	0	0	Predator	
	<i>Lithobius lucifugus</i>	4	4	0	8	0	1	Predator	
	<i>Lithobius tricuspis</i>	38	15	0	0	0	0	Predator	
<b>Diplopoda</b>	<i>Bergamosoma canestrinii</i>	28	30	4	0	0	0	Decomposer	
	<i>Leptoiulus alemannicus</i>	8	11	0	0	0	0	Decomposer	
	<i>Leptoiulus helveticus</i>	2	0	0	0	10	1	Decomposer	
	<i>Leptoiulus riparius</i>	4	0	1	0	0	0	Decomposer	
	<i>Ophiulus nigrofuscus</i>	0	1	0	0	0	0	Decomposer	
	<i>Orthochordeumella pallida</i>	7	9	0	1	0	0	Decomposer	
	<i>Pseudocraspedosoma grypischium</i>	0	149	0	62	0	0	Decomposer	
	<i>Pterygophorosoma alticolum</i>	53	0	71	698	59	508	Decomposer	
<b>Collembola</b>	<i>Arrhopalites pygmaeus</i>	496	362	437	221	9	166	Decomposer	[4]
	<i>Ceratophysella denticulata</i>	0	1	1	1	0	0	Generalist	[5-8]
	<i>Ceratophysella engadinensis</i>	2	67	0	1	0	27	Generalist	[5-8]
	<i>Choreutinula inermis</i>	1	0	5	0	0	0	Generalist	[9]
	<i>Desoria saltans</i>	14	21	10	26	0	1	Decomposer	[10]
	<i>Deuterostminthurus pallipes</i>	3	0	0	0	1	0	Herbivorous	[11]

	<i>Hypogastrura papillata</i>	0	0	6	0	0	0	Decomposer	[9]
	<i>Kalaphorura burmeisteri</i>	44	38	81	49	18	51	Generalist	[12]
	<i>Lepidocyrtus curvicollis</i>	4	0	0	0	0	0	Decomposer	[13]
	<i>Lepidocyrtus lignorum</i>	108	5	36	15	106	9	Decomposer	[13-14]
	<i>Lepidocyrtus violaceus</i>	454	140	14	31	55	5	Decomposer	[14]
	<i>Megalothorax minimus</i>	143	0	0	0	0	0	Decomposer	[15]
	<i>Neelus murinus</i>	64	9	24	48	5	20	Decomposer	[16-18]
	<i>Orchesella flavescens</i>	0	9	0	0	0	0	Decomposer	[19]
	<i>Orchesella quinquefasciata</i>	3	28	0	0	0	0	Generalist	[20]
	<i>Protaphorura armata</i>	39	2	0	1	10	2	Generalist	[6]
	<i>Pseudachorutes sp.</i>	0	1	0	0	0	0	Decomposer	[21]
	<i>Tomocerus minor</i>	28	2	30	3	0	11	Generalist	[22]
<b>Diplura</b>									
	<i>Plusiocampa caprai</i>	20	16	0	0	2	1	Decomposer	[23]
<b>Carabidae</b>									
	<i>Leistus montanus rhaeticus</i>	0	0	0	0	0	1	Predator	
	<i>Nebria breinii</i>	2	3	227	188	0	172	Predator	
	<i>Nebria castanea</i>	0	0	0	0	1	2	Predator	
<b>Staphylinidae</b>									
	<i>Acidota crenata</i>	0	0	0	1	0	0	Generalist	[24]
	<i>Acidota cruentata</i>	0	1	0	0	0	0	Generalist	[24]
	<i>Aloconota currax</i>	0	0	0	0	0	1	No info. avail.	
	<i>Amischa sp.</i>	0	0	1	0	0	0	No info. avail.	
	<i>Anthophagus spectabilis</i>	0	1	1	0	0	0	Generalist	[25]
	<i>Atheta contristata</i>	1	1	0	0	0	0	Generalist	[26]
	<i>Atheta europaea</i>	0	0	0	1	0	1	Generalist	[26]
	<i>Atheta laevicauda</i>	0	0	0	0	0	1	Generalist	[26, 27]
	<i>Bryaxis judicariensis</i>	8	0	0	0	0	0	Predator	[28]

<i>Bryaxis sculpticornis</i>	11	43	0	0	0	0	Predator	[28]
<i>Enalodroma hepatica</i>	0	1	0	0	0	0	No info. avail.	
<i>Leptusa areraensis</i>	86	28	219	1	1	0	Predator	[29]
<i>Leptusa</i> sp. new	0	1	0	0	2	0	Predator	[29]
<i>Lesteva longoelytrata</i>	0	0	0	0	0	3	Predator	[30]
<i>Lesteva luctuosa</i>	1	0	0	0	0	0	Predator	[30]
<i>Liogluta alpestris</i>	0	0	0	0	1	0	No info. avail.	
<i>Liogluta microptera</i>	0	0	0	0	1	0	No info. avail.	
<i>Mycetoporus baudueri</i>	1	0	0	0	0	0	No info. avail.	
<i>Neuraphes frigidus austriacus</i>	2	2	0	0	0	0	Predator	[31]
<i>Omalium septentrionis</i>	0	0	0	1	0	0	Generalist	[32]
<i>Omalium validum</i>	3	0	0	0	0	0	Generalist	[33]
<i>Oxypoda densa</i>	5	0	1	0	7	0	Generalist	[31]
<i>Quedius mesomelinus</i>	0	1	0	0	0	0	Predator	[34]
<i>Stenus glacialis</i>	0	0	0	1	1	0	Predator	[35]
<i>Trichophya pilicornis</i>	1	0	0	0	0	0	Decomposer	[35]

## References to Table S3

1. Dioli, P., Foianini, I. & Tognini, P. Presenza dell'opilionide calcifilo *Dicranopalpus gasteinensis* Doleschal, 1852 (Aracnida, Opiliones, Phalangidae) nelle grotte della Valmalenco (Provincia di Sondrio, Lombardia, Italia settentrionale). *Il Naturalista Valtellinese – Mus. Civ. Stor. Nat. Morbegno* **23**, 5–14 (2012).
2. Schoenhofer, A. L., & Martens, J. On the identity of *Ischyropsalis dentipalpis* Canestrini, 1872 and description of *Ischyropsalis lithoclasica* sp. n. (Opiliones: Ischyropsalididae). *Zootaxa* **2613(1)**, 1–14 (2010).
3. Schmidt, M., Achterhold, K., Pfeiffer, F. & Melzer, R. Kinematics of elongate harvestmen chelicerae: Comparative range of motion analyses in extant *Ischyropsalis* (Dyspnoi, Opiliones). *Zool.* **167**, 126219 (2024).
4. Hågvar, S. & Hågvar, E. B. Invertebrate activity under snow in a South-Norwegian spruce forest. *Soil org.* **83(2)**, 187–209 (2011).
5. Zettel, J., Zettel, U., Suter, C., Streich, S. & Egger, B. Winter feeding behaviour of *Ceratophysella sigillata* (Collembola: Hypogastruridae) and the significance of eversible vesicles for resource utilisation: Proceedings of the Xth international Colloquium on Apterygota, České Budějovice 2000: Apterygota at the Beginning of the Third Millennium. *Pedobiologia* **46(3-4)**, 404–413 (2002).
6. Ferlian, O., Klarner, B., Langeneckert, A. E. & Scheu, S. Trophic niche differentiation and utilisation of food resources in collembolans based on complementary analyses of fatty acids and stable isotopes. *Soil Biol. Biochem.* **82**, 28–35 (2015).
7. Kataoka, M. & Nakamori, T. Food preferences of Collembola for myxomycete plasmodia and plasmodium responses in the presence of Collembola. *Fungal Ecol.* **47**, 100965 (2020).
8. Lu, J. Z. et al. Trophic niche variation in springtails across soil depth. *European Journal of Soil Biol.* **126**, 103745 (2025).
9. Potapov, A. M., Pollierer, M. M., Salmon, S., Šustr, V. & Chen, T. W. Multidimensional trophic niche revealed by complementary approaches: Gut content, digestive enzymes, fatty acids and stable isotopes in Collembola. *J. Anim. Ecol.* **90(8)**, 1919–1933 (2021).
10. Valle, B. et al. The unexplored biodiversity of 'glacier fleas' (Hexapoda: Collembola): Taxonomy, distribution and ecology in the European Alps and Apennines. *J. Zool. Syst. Evol. Res.* **2025(1)**, 1616350 (2025).
11. Ellis, W. N. Pollen feeding of *Deuterostminthurus repandus* (Agren) in the High Pyrenees, and some systematic notes (Collembola: Sminthuridae). *Entomol. Ber.* **38(4)**, 61–63 (1978).
12. Fiera, C. Application of stable isotopes and lipid analysis to understand trophic interactions in springtails. *North-West. J. Zool.* **10(2)**, 227–235 (2014).

13. Crotty, F. V. & Adl, S. M. Competition and predation in soil fungivorous microarthropods using stable isotope ratio mass spectrometry. *Front. Microbiol.* **10**, 1274 (2019).
14. Kuehn, J., & Ruess, L. Effects of resource quality on the fitness of collembola fed single and mixed diets from the green and brown food chain. *Soil Biol. Biochem.* **154**, 108156 (2021).
15. Gillet, S. & Ponge, J. F. Species assemblages and diets of Collembola in the organic matter accumulated over an old tar deposit. *Eur. J. Soil Biol.* **41(1-2)**, 39–44 (2005).
16. Folsom, J. W. Review of the Collembolan genus *Neelus* and description of *N. minutus* n. sp. *Psyche* **9(303)**, 219–222 (1901).
17. Kováč, L. & V. Papáč. Revision of the genus *Neelus* Folsom, 1896 (Collembola, Neelida) with the description of two new troglobiotic species from Europe. *Zootaxa* **2663**, 36–52 (2010).
18. Papáč, V., Lukić, M., & Kováč, L. (2016). Genus *Neelus* Folsom, 1896 (Hexapoda, Collembola) reveals its diversity in cave habitats: two new species from Croatia. *Zootaxa* **4088(1)**, 51–75.
19. Anderson, J. M. & Healey, I. N. Seasonal and inter-specific variation in major components of the gut contents of some woodland Collembola. *J. Anim. Ecol.* **41(2)**, 359–368 (1972).
20. Berg, M. P., Stoffer, M. & van den Heuvel, H. H. Feeding guilds in Collembola based on digestive enzymes. *Pedobiologia* **48(5-6)**: 589–601 (2004).
21. Chahartaghi, M., Langel, R., Scheu, S. & Ruess, L. Feeding guilds in Collembola based on nitrogen stable isotope ratios. *Soil Biol. Biochem.* **37(9)**, 1718–1725 (2005).
22. Verhoef, H. A., Prast, J. E. & Verweij, R. A. Relative importance of fungi and algae in the diet and nitrogen nutrition of *Orchesella cincta* (L.) and *Tomocerus minor* (Lubbock)(Collembola). *Funct. Ecol.* **2(2)**, 195–201 (1988).
23. Sendra, A., Palero, F., Jiménez-Valverde, A. & Reboleira, A. S. P. Diplura in caves: diversity, ecology, evolution and biogeography. *Zool. J. Linn. Soc.* **192(3)**, 675–689 (2021).
24. Belskaya, E. A., & Kolesnikova, A. A. Species composition and ecological characteristics of rove beetles (Coleoptera, Staphylinidae) in the southern taiga of the Middle Urals. *Entomol. Rev.* **91(5)**, 599–610 (2011).
25. Shavrin, A. On the genus *Anthophagus* Gravenhorst, 1802 (Coleoptera: Staphylinidae, Omaliinae, Anthophagini) in Cisbaikalia, with additional Palaearctic material of *A. (Phaganthus) caraboides* Linnaeus, 1758. *Balt. J. Coleopterol.* **8(2)**, 159–167 (2008).

26. Glotov, S., Hushtan, K., Hushtan, H., Koval, N., Diedus, V. The Genus *Atheta* (Coleoptera, Staphylinidae, Aleocharinae) in the Ukrainian Carpathians. *Zoodiversity* **56(2)**, 91–110 (2022).
27. Stefani, F. O. et al. Fungal community composition in the gut of rove beetles (Coleoptera: Staphylinidae) from the Canadian boreal forest reveals possible endosymbiotic interactions for dietary needs. *Fungal Ecol.* **23**, 164–171 (2016).
28. Tamutis, V. & Skłodowski, J. Coleoptera assemblages of pine forests depends on the distance to the source of nitrogen pollution. *Community Ecol.* **17(2)**, 225–236 (2016).
29. Orlov, I., Solodovnikov, A., & Leschen, R. A. Systematics and biogeography of the subantarctic *Leptusa* (Coleoptera: Staphylinidae: Aleocharinae: Homalotini). *Syst. Biodivers.* **17(1)**, 60–79 (2019).
30. Svobodová, Z., Habuštová, O. S., Boháč, J. & Sehnal, F. Functional diversity of staphylinid beetles (Coleoptera: Staphylinidae) in maize fields: testing the possible effect of genetically modified, insect resistant maize. *Bull. Entomol.* **106(4)**, 432–445 (2016).
31. Betz, O., Irmeler U. & Klimaszewski J. *Biology of rove beetles (Staphylinidae) - life history, evolution, ecology and distribution* (Springer, 2018).
32. Szafraniec, S., ChachuŁA, P., Melke, A., Ruta, R., & SzoŁTys, H. New findings of rare and interesting beetles (Coleoptera) in the Babia Góra National Park. *Wiad. Entomol.* **38**, 212–231 (2019).
33. Kocot-Zalewska, J., & Lis, B. Species Composition and Structure of Beetle Associations in Caves of the Częstochowa Upland, Poland. *Diversity* **15(3)**, 345 (2023).
34. Parimuchová, A., et al. The food web in a subterranean ecosystem is driven by intraguild predation. *Sci. Rep.* **11(1)**, 4994 (2021).
35. Ashe, J. S., & Newton Jr, A. F. Larvae of *Trichophya* and phylogeny of the tachyporine group of subfamilies (Coleoptera: Staphylinidae) with a review, new species and characterization of the Trichophyinae. *Syst. Entomol.* **18(4)**, 267–286 (1993).

**Table S4.** Relative abundance of fungal OTUs at each sampling site in the debris layers of three habitats (rock glacier, glacier foreland and lateral scree field) in two neighbouring valleys (Val Sassa and Valletta) in the Swiss National Park in the Eastern Alps. Mean values of five different depths are given for each sampling site. Codes for sampling sites are in Table S2. The means of the samples taken at five depths are presented.

	SR1	SR2	SR3	SR4	SF1	SF2	SL1	SL2	VR1	VR2	VR3	VR4	VF1	VF2	VL1	VL2
bp391/392	5,29	5,29	5,29	5,29	4,26	5,32	5,29	5,29	5,29	5,29	5,30	5,29	5,29	5,29	5,29	5,29
bp394/395	12,30	10,62	15,32	11,17	27,52	40,61	2,11	14,60	8,62	16,69	16,53	11,64	14,25	3,53	17,33	2,01
bp396/397	4,22	3,06	7,70	8,94	16,06	1,39	9,95	3,11	6,79	6,34	5,52	17,78	0,94	1,95	5,43	15,01
bp399	36,37	15,84	6,79	3,65	6,21	17,79	16,31	0,46	0,57	9,57	8,94	1,43	18,32	1,21	6,06	0,52
bp401	7,16	12,55	4,91	8,19	2,28	2,90	2,49	14,18	11,04	15,09	9,14	1,55	24,55	41,20	7,05	1,02
bp403	4,98	0,00	0,00	0,00	0,00	0,00	2,24	1,95	2,34	5,72	2,45	0,00	3,33	8,28	6,57	8,82
bp405/406	0,90	7,89	28,66	11,29	7,44	4,02	8,94	0,27	5,50	0,00	3,75	3,72	0,97	4,97	3,12	4,31
bp407	0,20	1,24	0,42	0,00	0,24	0,00	0,00	0,25	0,06	1,10	0,28	0,00	1,78	0,00	0,36	0,09
bp408/409	0,85	0,16	0,80	7,20	2,13	2,65	0,20	1,94	0,00	3,52	1,66	0,38	0,67	21,28	11,36	7,87
bp410	0,15	0,82	0,08	0,49	0,18	2,34	6,06	4,90	1,57	7,59	4,49	9,98	3,25	0,00	1,35	10,87
bp413	12,51	0,00	0,08	7,13	0,00	0,00	0,17	0,04	0,32	5,52	1,21	1,75	1,57	0,91	0,36	0,31
bp416	0,00	0,47	0,09	0,20	3,07	0,09	8,48	0,77	5,95	0,61	3,18	2,28	0,05	0,11	0,06	6,90
bp419	0,11	1,91	0,16	1,69	0,00	4,45	16,02	5,48	1,01	8,04	7,00	0,44	0,86	2,98	4,00	1,12
bp422	1,00	3,13	0,86	2,74	0,00	0,30	0,00	2,26	5,26	0,00	1,56	2,90	0,38	0,18	0,08	0,90
bp425	1,08	1,41	1,96	0,17	10,51	0,00	4,24	0,00	0,09	0,00	0,87	6,62	1,18	1,04	0,77	3,20
bp427	0,13	3,20	2,89	0,30	0,17	3,43	5,86	17,25	11,67	5,96	8,83	5,30	1,53	5,87	4,72	1,85
bp429	7,62	1,59	0,71	0,00	0,18	0,38	0,00	0,53	0,80	0,00	0,34	2,50	1,42	0,89	4,28	0,00
bp431	0,67	2,55	0,64	8,68	3,41	9,03	2,03	8,41	4,52	2,22	5,24	1,78	1,56	0,64	1,32	1,98
bp433	0,00	0,00	0,00	0,00	0,00	0,18	0,00	0,23	0,24	0,00	0,13	0,00	0,00	0,00	0,15	0,00
bp434/435	0,85	1,31	0,81	1,88	1,13	1,18	0,00	4,26	23,78	2,19	6,28	3,42	1,80	0,42	3,37	0,45
bp436	0,00	0,80	0,04	0,90	2,07	0,21	1,85	2,93	3,14	3,95	2,42	1,21	0,40	0,28	3,12	2,15
bp439/440	0,18	0,32	0,10	0,26	3,77	0,60	0,80	1,76	1,11	0,54	0,96	5,07	1,32	0,00	0,81	1,40



bp505	0,00	0,00	0,04	0,00	0,00	0,00	0,00	0,12	0,00	0,00	0,02	0,00	0,00	0,00	0,07	0,86
bp509	0,00	0,00	0,00	0,00	0,25	0,00	0,00	0,04	0,00	0,00	0,01	0,12	0,00	0,00	0,00	0,00
bp523	0,00	0,00	0,00	0,00	0,00	0,08	0,00	0,00	0,00	0,00	0,02	0,08	0,00	0,00	0,61	0,67
bp533	0,00	0,16	0,00	0,27	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
bp536	0,00	0,00	0,00	0,00	0,00	0,08	0,00	0,00	0,00	0,00	0,02	0,00	0,00	0,00	0,00	0,00
bp543	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,57	0,00	0,00	0,00	0,00
bp560	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
bp572	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
bp576	0,00	0,00	0,00	0,00	0,00	0,00	0,11	0,14	0,00	0,00	0,05	0,12	0,00	0,14	0,07	0,31
bp608	0,00	0,00	0,00	0,00	0,14	0,13	0,00	0,00	0,00	0,00	0,03	0,00	0,00	0,00	0,00	0,00
bp614	0,00	0,00	0,00	0,00	0,00	0,08	0,00	0,00	0,00	0,00	0,02	0,00	0,00	0,00	0,00	0,00
bp618	0,12	0,00	0,04	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
bp620	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,03	0,00	0,00	0,01	0,07	0,00	0,00	0,00	0,00
bp671	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,38	0,00	0,00	0,00

---



<i>Moehringia ciliata</i>	0	0	0	0	0	0	1	1,01	0	1	2	1,02	0	0
<i>Papaver alpinum</i>	0	0	3	1,02	0	1	1	0	0	0	0	0	0	0
<i>Poa alpina</i>	0	0	0	0	2,05	5	0	0	0	0	0	0	0	0
<i>Poa glauca</i>	0	0	0	0	0	0	0	5	1,01	1	1	1,02	0	0
<i>Polygonum viviparum</i>	0	0	0	0	0	2	0	0	0	0	0	0,01	0	0
<i>Ranunculus glacialis</i>	0	0	0	0	0	0	0	0	0	0	2	5,01	0	0
<i>Salix helvetica</i>	0	0	0	0	0	0	0	0	0	0	9	0	0	0
<i>Saxifraga aizoides</i>	10	11	1	0	0,02	2,51	0	0	0	0	0	0	0	0
<i>Saxifraga oppositifolia</i>	0,03	2,51	1	1	0,01	0,01	1	0	1	1,01	0	0	0	0
<i>Saxifraga paniculata</i>	0	1	0	0	0	2	0	0	0	0	0	0	0	0
<i>Sedum atratum</i>	0	0	0	0	0	0	0	0	0	0	0,01	0,01	0	0
<i>Silene vulgaris</i>	15	10	0,01	0	0,02	6	0	0	0	0	0	0	0	0
<i>Veronica aphylla</i>	0	0,01	0,01	0	0	0	0	0	0	0	0	0	0	0
<i>Veronica fructicosa</i>	0	0	0	0	0	0	0	0	1	0	0	0,02	0	0

**Table S6.** Results of Spearman-rank correlation analyses examining the relationships between individual habitat characteristics and various diversity measures for each species group. Significant relationships are indicated in bold.

	Elevation	Mean temperature	Moss cover	Plant cover	pH
<b>Vascular plants (36 sp.)</b>					
Species richness	–	$r_s = -0.489, P = 0.054$			<b><math>r_s = -0.719, P = 0.002</math></b>
Shannon diversity index	–	$r_s = -0.466, P = 0.068$			
Evenness	–	–	–		
<b>Invertebrates (80 species)</b>					
Species richness	–	–	$r_s = -0.442, P = 0.082$		$r_s = -0.090, P = 0.730$
Rarefied species richness	–	–	$r_s = -0.482, P = 0.068$		
Abundance	$r_s = 0.073, P = 0.788^a$	–	<b><math>r_s = -0.506, P = 0.045</math></b>		
Shannon diversity index	–	–			
Evenness	–	–	–		
<b>Arthropods excluding insects (30 species)</b>					
Species richness	–	$r_s = -0.491, P = 0.059$	$r_s = -0.167, P = 0.552$	$r_s = -0.101, P = 0.703$	
Rarefied species richness	–	<b><math>r_s = -0.515, P = 0.041</math></b>	$r_s = -0.092, P = 0.734$	–	
Abundance	–	–	<b><math>r_s = -0.593, P = 0.016</math></b>	$r_s = -0.373, P = 0.155$	
Shannon diversity index	–	–			
Evenness	–	$r_s = 0.133, P = 0.624^a$	$r_s = 0.463, P = 0.0571$		
<b>Insects (48 species)</b>					
Species richness	–	–			
Rarefied species richness	–	–			
Abundance	<b><math>r_s = -0.594, P = 0.017</math></b>	–			
Shannon diversity index	–	$r_s = 0.435, P = 0.059$			
Evenness	–	–			

<sup>a</sup> U-shaped relationship

In all cases  $n = 16$

**Table S7.** Percentages of invertebrates (%) in different functional feeding groups in the debris layers of rock glaciers, forelands and lateral scree fields. Data from the Val Sassa and Valletta valleys are combined. The species are weighted based on the number of individuals caught. Species whose functional group is unknown were not included in the statistical analysis.

	Rock glacier	Foreland	Lateral scree field
Predators	18.6	14.7	27.3
Herbivores	0.1	0.1	0
Decomposers	75.3	72.3	59.1
Generalists	5.9	12.6	13.5
Species with missing information	0.1	0.3	0.1

$\text{Chi}^2 = 95.22, \text{df} = 6, P < 0.0001$