

Biodiversity in mountain soils above the treeline

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84 **ABSTRACT**

85 Despite the importance of healthy soils for human livelihood, wellbeing, and safety, current gaps in our
86 knowledge and understanding of biodiversity in soil are numerous, undermining conservation efforts. These
87 gaps are particularly wide in mountain regions where healthy soils are especially important for human
88 safety and yet evidence is accumulating of ongoing degradation, posing significant threats to ecosystem
89 functioning and human settlements.

90 To analyse these gaps in detail, we synthesise current research on the global diversity of microorganisms,
91 cryptogams, and invertebrates in mountain soils above the treeline. This synthesis is based on a semi-
92 quantitative survey of the literature and an expert-based analysis. Our work reveals not only deficiencies in
93 geographic cover but also significant gaps in taxonomic coverage, particularly among soil protists and
94 invertebrates, and a lack of (functional and ecological) description of the uncultivated majority of
95 prokaryotes, fungi, and protists. We subsequently build on this overview to highlight opportunities for
96 research on mountain soils as systems of co-occurring species that interact in complex environmental
97 matrices to fulfil critical functions and make essential contributions to life on land.

98 Closing gaps in biodiversity research in mountain soil is crucial to enhance our understanding and to
99 promote laws and guidelines advancing international soil biodiversity conservation targets in mountains.
100 Addressing sparse and biased data, recognizing the impact of environmental changes on mountain
101 ecosystems, and advocating dedicated policies are essential strategies to safeguard mountain soils and their
102 biodiversity.

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105 *Keywords:* alpine soils, bacteria, biogeography, bryophytes, cryptogams, fungi, lichens, microbial diversity,
106 protists, soil fauna

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108 **GLOSSARY**

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Term	Chapter	Definition
acidophile	General	Organisms which favour low pH conditions; especially regarding growth and reproduction
aeolian food source	General	Any kind of organic material that is transported by wind and that can serve as a nutrient source
alkaliphile	General	Organisms which favour high pH conditions; especially regarding growth and reproduction
autotrophic	General	Ability to produce biomass solely by using inorganic substances; often refers to C-autotrophy when using inorganic C compounds, such as CO ₂ , for synthesis of biomass-C
brachyptery	Soil fauna	Describes an anatomical condition where winged animals (mostly insects) have very short and/or non-functional wings. This can be sex-specific (e.g. often found in females) or be related to environmental conditions (e.g. cold, windy)
bryophytes	Cryptogams	Non-vascular plants that include mosses, hornworts, and liverworts
cetrarioid lichen	Cryptogams	Monophyletic group of lichens that either belong to or are closely related to the genus <i>Cetraria</i>
chasmolithic	Cryptogams	Growing in rock cracks
chionophilous	Cryptogams	Organisms which prefer or need a permanent snow cover
chionophobic	Cryptogams	Organisms which avoid snow-covered habitats
cryophilous	Cryptogams	Organisms which prefer very low temperatures
ecotone	General	Transition between ecological communities, ecosystems, and/or ecological regions along an environmental gradient
endemic	General	Native and restricted to a certain place
endophyte	Soil microbiota	Organisms, mostly fungi or bacteria, living within a plant without causing a disease
epiphyte	General	Growing on plants
eukaryotes, eukaryotic	General	Organisms with cell nucleus; protists, animals, fungi, plants
eurihydric	Cryptogams	Ability to withstand a wide range of humidity
fruticose	Cryptogams	Fruticose lichens have a three-dimensional, shrub-like or bushy growth pattern
halophile	General	Organisms which favour high salt concentrations; especially regarding growth and reproduction
liverwort	Cryptogams	A non-vascular bryophyte that belongs to the division Marchantiophyta

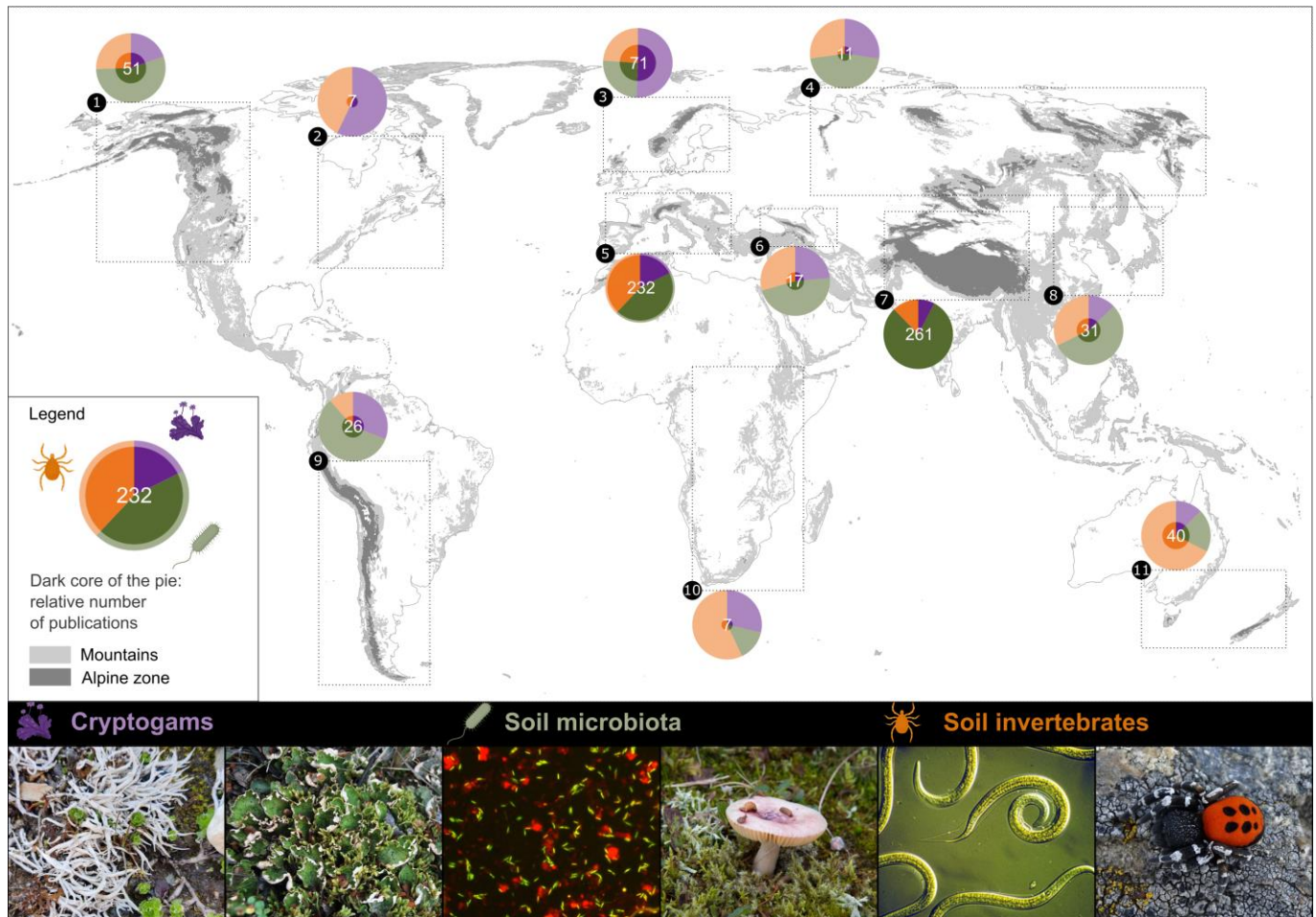
neutrophile	General	Organisms which favour neutral pH conditions; especially regarding growth and reproduction
nitrogen fixation	Soil microbiota	The biotic energy consuming process by which inorganic N ₂ is converted to NH ₃ ; only performed by bacteria and archaea
nunatak	General	Mountain summits and ridges that remained ice-free during the last Ice Age and served as refuges for alpine and high alpine fauna, flora, and microbiota
petrophile	Soil fauna	Organisms which favour rocky environments
phanerogam	Cryptogams	Plants that produce seeds. Also termed as spermatophytes
pleurocarpous moss	Cryptogams	Mosses in which the sporophyte is borne on short lateral branches and not culminating the growth of the main axes (i.e. acrocarpous moss)
poikilohydric	Cryptogams	Organism whose water status is passively controlled by the environment
prokaryote, prokaryotic	Soil microbiota	Organisms without cell nucleus; archaea and bacteria
protist	Soil microbiota	All eukaryotes that are not plants, metazoans, or fungi
psychrophile	General	Organisms which favour low temperature conditions; especially regarding growth and reproduction
rhizosphere	Soil microbiota	Narrow space/region in the soil directly influenced by plant roots
saprotrophic	General	An organism that feeds on dead organic matter
saxicolous	Cryptogams	Growing on rock
soil microbiota	Soil microbiota	Prokaryotes, fungi, and protists living in soil
terricolous	Cryptogams	Growing on soil
thermophile	General	Organisms which favour high temperature conditions; especially regarding growth and reproduction

111 I. INTRODUCTION

112 In recent years, our awareness of the importance of soils and their biodiversity has steadily increased,
113 pressed by the growing evidence of rapid soil degradation worldwide and across all biomes (European
114 Environment Agency, 2019; FAO *et al.*, 2020; Anthony, Bender & van der Heijden, 2023). Because of
115 their environmental, societal, and economic consequences, soil degradation and the loss of soil biodiversity
116 pose a major threat to humankind. The need to protect soils has become an international priority (IPBES,
117 2018), reflected in both the Agenda for Sustainable Development of the United Nations and the recently
118 adopted Kunming-Montreal Global Biodiversity Framework (United Nations, 2015; UN Convention on
119 Biological Diversity, 2022). The demand for data, knowledge, and global responses to the challenge of how
120 to safeguard soils and their biota has led to an increasing number of international initiatives, including the
121 Soil Biodiversity Observation Network (SoilBON), the Global Soil Biodiversity Initiative (GSBI), the
122 International Network on Soil Biodiversity (NETSOB), and the Global Soil Laboratory Network
123 (GLOSOLAN). All these initiatives aim at providing the biological and ecosystem information needed to
124 implement sustainable management and conservation of soils.

125 Despite these recent developments, major gaps and blind spots still exist in soil research and in available
126 data and knowledge on soil biodiversity. This is particularly the case with mountains (Baruck *et al.*, 2016;
127 Guerra *et al.*, 2020), even though mountain soils are critical for many ecosystem processes, functions, and
128 services, and their maintenance and stability are particularly important in terms of hazards and natural risk
129 management (FAO, 2015; Stanchi *et al.*, 2023). Given that mountain soils can take thousands of years to
130 develop (up to 1000 years for 2–3 cm in (high) alpine areas (Stanchi *et al.*, 2023), their degradation and
131 gradual erosion as a result of overexploitation and poor management may ultimately lead to a loss of
132 biodiversity and associated ecosystem collapse, with no option for recovery (Körner, 2021; Singh *et al.*,
133 2023). It emphasises the complexity of ecological restoration, pointing out that while repairing functions
134 and maintaining existing taxa is feasible to some extent, the irreversible loss of certain locally adapted
135 species, especially in isolated environments like nunataks, is a significant concern. These threats are further
136 exacerbated by climate and land-use change, as well as the increasing occurrence of invasive non-native
137 species (Palomo, 2017; Zucconi & Buzzini, 2021; Iseli *et al.*, 2023). Here, we first provide a synthetic
138 overview of the current state of knowledge on biodiversity in mountain soils above the treeline. We
139 subsequently build on this overview to highlight opportunities for research on mountain soils as systems of
140 co-occurring species that interact in complex environmental matrices to fulfil critical functions and make
141 essential contributions to life on land. We restrict this review to alpine soils above the treeline in mountain
142 regions (Fig. 1, Table 1). The term ‘alpine’ in this context specifically refers to soils located in mountainous
143 areas above the treeline. The synthesis was performed as a collaborative effort by members of the Global
144 Mountain Biodiversity Assessment (GMBA) ‘Mountain Soil Biodiversity’ working group, who

145 summarised current literature in their respective fields of expertise. This body of literature was further
 146 consolidated based on a semi-comprehensive review of available publications.
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 149 **Fig. 1.** Global map of the number of scientific papers on biodiversity in mountain soils above the treeline
 150 (cryptogams, soil microbiota, and soil invertebrates) by alpine region. The dark core of the pies represents
 151 the number of publications in the respective area compared to the number of the region with the most
 152 publications (i.e. Central Asia). The alpine regions were named here as (1) North American Cordillera, (2)
 153 Appalachians & Northeast Ranges, (3) Northern Europe, (4) North Asia, (5) Central & Southern Europe,
 154 (6) Caucasus, (7) Central Asia, (8) East Asia, (9) Andes & South America, (10) Afro-alpine Region, and
 155 (11) Australia & New Zealand. See Fig. S1 for an alternative version showing the density of papers per km²
 156 of alpine area. Photos from left to right: Cryptogams: Arctic-alpine lichen *Thamnolia vermicularis*, arctic-
 157 alpine lichen *Peltigera aphthosa* (credit: Bettina Weber); Soil microbiota: DNA stained microscope
 158 preparation of soil bacteria (credit: Nadine Praeg & Paul Illmer), *Russula* sp. (credit: Andrea J. Britton);
 159 Soil invertebrates: Nematodes and a male velvet spider *Eresus sandaliatus* (credits: CSIRO Entomology
 160 and Michael Steinwandter, respectively).

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164 **Table 1.** List of the alpine mountain regions included in this review, presenting their respective area, and
 165 the corresponding number of papers per main soil organism group. The identification (ID) numbers of the
 166 alpine mountain regions align with those referenced in the Figs. 1 & 3–5. The designation of the regions
 167 identified as ‘alpine region’ along with a summary of the corresponding mountain ranges is detailed in
 168 Table S3. For visual comparison of the areas (tree map) of the alpine mountain regions, please refer to Fig.
 169 S2 in Appendix S1.

Nr.	Alpine region	Area [km ²]	Number of scientific articles			
			Cryptogams	Microbes	Invertebrates	<i>Total</i>
1	North American Cordillera	306,815	10	28	13	<i>51</i>
2	Appalachians & Northeast Ranges	10,929	4	0	3	<i>7</i>
3	Northern Europe	47,623	36	18	17	<i>71</i>
4	North Asia	395,738	3	5	3	<i>11</i>
5	Central & Southern Europe	26,606	41	103	88	<i>232</i>
6	Caucasus	16,567	4	8	5	<i>17</i>
7	Central Asia	2,188,571	20	209	32	<i>261</i>
8	East Asia	2,778	4	17	10	<i>31</i>
9	Andes & South America	547,091	8	15	3	<i>26</i>
10	Afro-alpine Region	497	2	1	4	<i>7</i>
11	Australia & New Zealand	12,639	5	8	27	<i>40</i>
	Sums	3,555,854	137	412	205	<i>754</i>

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172 **II. METHODS**

173 The synthesis was performed by querying ‘Web of Science’ for scientific papers on biodiversity in
174 mountain soils in the alpine zones of the world (i.e. above the treeline in temperate and continental climatic
175 zones, excluding tropical areas) and attributing each paper to one or more of the organismic groups
176 considered here, making a distinction between primary and secondary focus as many publications covered
177 more than one organismic group (Figs. 3–5) (see detailed methods in Appendix S1). Each paper was also
178 attributed to one of the 11 defined alpine regions (see Table 1 and Table S3) according to the mountain
179 ranges or systems that were specified in the title, abstract, keywords, or methods. The lists were
180 subsequently reviewed and validated and supplemented with references from the authors personal reference
181 databases. See Appendix S1 for a detailed description of the literature search and data processing.

183 **III. CHARACTERISTICS OF MOUNTAIN ZONES ABOVE THE TREELINE**

184 **(1) Soil**

185 Major soil types occurring in the alpine and nival zones of temperate and continental mountains include
186 (according to the soil taxonomy, Soil Survey Staff, 2022) Entisols, Inceptisols, Mollisols, Histosols,
187 permafrost-affected soils, and Podzols, the latter mainly found on siliceous rocks, slopes with conifers, and
188 alpine dwarf-shrub zones (Gelisols) (Price & Harden, 2013). Soil formation in mountain areas is – besides
189 climatic factors – typically controlled by microrelief and morphodynamics, gravitational and fluvial
190 dynamics, solifluction, and wind-related processes (Egli, Dahms & Norton, 2014). Accordingly, soil types
191 and properties show small-scale heterogeneity (Egli & Poulénard, 2016) resulting from the high variability
192 in (micro-) climate, topography, orientation, slope, and regional/local wind systems (Burga, Klötzli &
193 Grabherr, 2004; Hoorn, Perrigo & Antonelli, 2018). Properties that are specific to alpine soils include an
194 incomplete development (Donhauser & Frey, 2018), with slow humus accumulation and limited nutrient
195 supply, even though accumulation of wind-blown fine material may, on a small scale, improve the physical
196 and chemical characteristics of stony substrates (Gild, Geitner & Sanders, 2018). Detailed information on
197 mountain soil types and characteristics is an important prerequisite to understanding biodiversity in soil and
198 the unique adaptations of soil (micro-)organisms to overall hostile environmental conditions (Fig. 2)
199 (Pellissier *et al.*, 2014; Orgiazzi *et al.*, 2016; Yashiro *et al.*, 2016; Mod *et al.*, 2020; Seppey *et al.*, 2020).
200 However, this information remains rare (Baruck *et al.*, 2016; Guisan *et al.*, 2019) and needs to be
201 implemented through specific and targeted initiatives (e.g. the establishment of the Alpine Soil Partnership
202 in 2017).

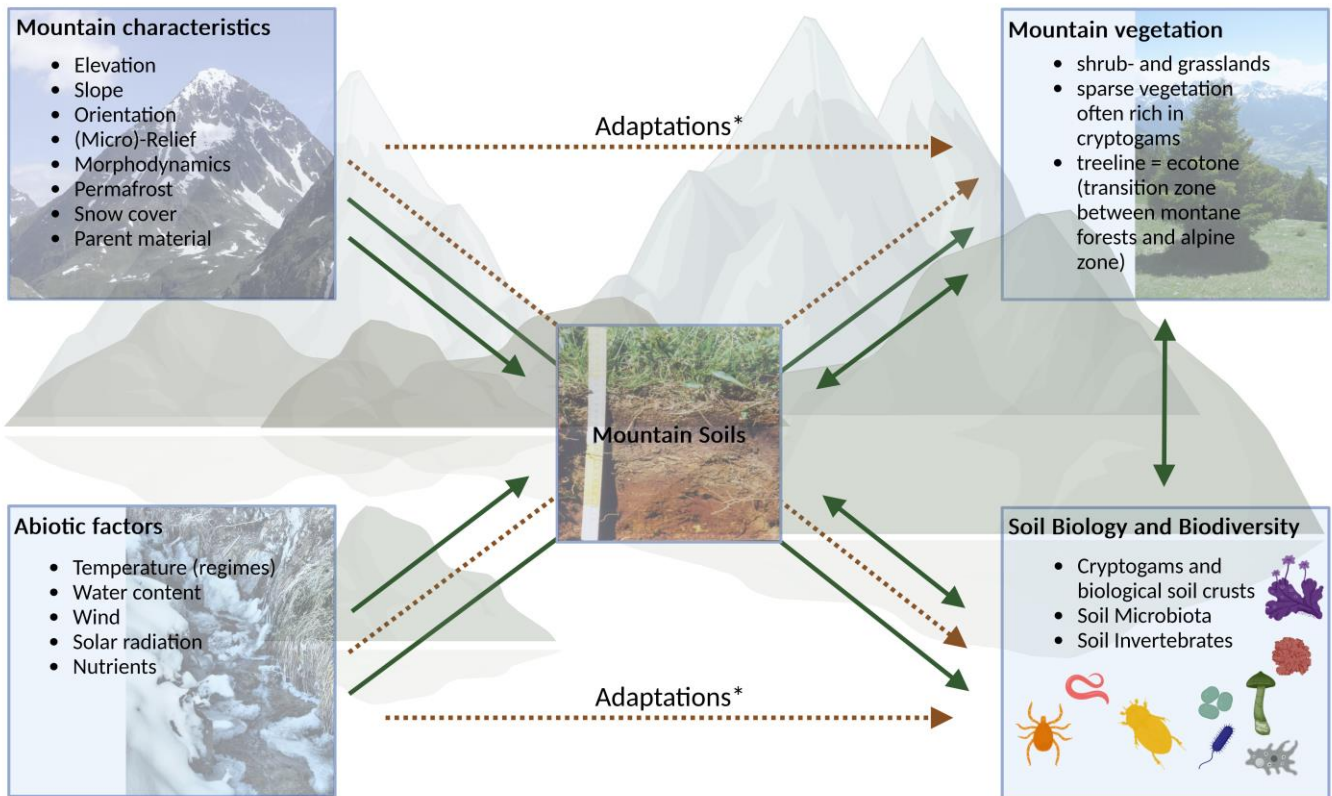
203 Generally, life in mountain soils is determined by their abiotic properties, including water content and
204 temperature as the main drivers of chemical and physical weathering, parent material, including chemical
205 composition, physical properties, resistance against weathering, and the predetermination of soil pH as well
206 as organic matter quality and quantity (Fig. 2) (Paul & Clark, 1996). Both the length of the growing season

207 and the mean temperature in mountain soils typically decrease with increasing elevation. In eastern
208 Scotland, for example, Britton *et al.* (2011) measured a decrease in mean summer soil temperature at 10 cm
209 depth from 9.5 °C at the treeline at 640 m a.s.l. to 7.2 °C at 908 m and a decline in the length of the growing
210 season from 198 to 156 days based on a threshold of 5 °C. The low temperatures typical of mountain soils
211 at high elevations favour the accumulation of organic matter through reduced decomposition rates, which
212 can result in large amounts of soil carbon (Praeg *et al.*, 2020). Accordingly, mountain regions have received
213 increasing attention for their contribution to terrestrial C storage (Hagedorn, Gavazov & Alexander, 2019;
214 Stanchi *et al.*, 2021). While nival (and alpine) soils exhibit minimal C stocks (Frey *et al.*, 2016; Adamczyk
215 *et al.*, 2019; Luláková *et al.*, 2019), soils at lower elevations, where temperatures and plant coverage are
216 higher, may act as larger C sinks.

217 An additional factor affecting life in mountain soils is the presence of a substantial and long-lasting snow
218 cover. Together, seasonal snowpack depth, duration, and melt-out control the onset and duration of the
219 growing season, mitigate low soil temperatures, and affect microbial activity, soil nutrient cycling, soil gas
220 fluxes, and pedogenesis (Freppaz *et al.*, 2017). These factors further determine community composition,
221 and their high spatial variability may enable the close co-occurrence of species adapted to differing
222 environmental conditions such as chionophilous and chionophobic taxa (Odland & Munkejord, 2008;
223 Carlson *et al.*, 2015; Niittynen & Luoto, 2018; Seeber *et al.*, 2021; Panchard *et al.*, 2023). In addition to
224 the presence of substantial (and natural) snow cover, further drivers of change in abiotic soil properties
225 include winter sports operations. These activities, such as the establishment and maintenance of (large) ski
226 areas, including levelling and grading operations, represent strong mechanical disturbance. This promotes
227 the breakdown of soil aggregates, causes the exposure of organic matter that was previously protected in
228 undisturbed soils (Gros *et al.*, 2004), and fosters soil erosion, which all together lowers the organic C
229 content (Delgado *et al.*, 2007; Negro *et al.*, 2013) and reduces the soil micropore porosity, with
230 consequences for soil aeration and water holding capacity (Pohl *et al.*, 2009). Additionally, artificial
231 snowmaking uses nucleating agents and water, often diverted from lakes and streams, which contain
232 mineral and organic compounds that are not present in natural snow. This provides an additional input of
233 solutes during snow melting (Wipf *et al.*, 2005; Roux-Fouillet, Wipf & Rixen, 2011), resulting in higher
234 soil pH and electrical conductivity (Delgado *et al.*, 2007; Freppaz *et al.*, 2013; Casagrande Bacchiocchi *et*
235 *al.*, 2019).

236 Considering the impact of global change, mountain soils are likely to undergo major transitions. Nival
237 soils, as stated above, can be expected to increasingly serve as C sinks with climate warming. They are
238 equally expected to become N sinks due to increased plant productivity under warmer conditions
239 (Steinbauer *et al.*, 2018). This holds especially true for barren or sparsely vegetated soils with low C and N
240 content, where increased plant growth and primary production clearly outweigh temperature-driven
241 increases in soil respiration (Hagedorn *et al.*, 2019). In contrast, distinct increases in C loss have also been

242 reported as a consequence of increased temperatures allowing lowland plants to colonise alpine
243 environments (Walker *et al.*, 2022). Thus, predictions about the amount and the dynamics of C and N
244 cycling in response to global warming can only be made on a basis of a better understanding of the complex
245 biotic and abiotic interactions in mountain soils (Fig. 2).



—•••••—> factors leading to the adaptation of organisms —> influence

* dormancy, storage of carbohydrates in roots/rhizomes, lipids in old leaves, size (reduction), changed metabolic rates

247
248 **Fig. 2.** Overview of mountain characteristics and abiotic factors, influencing alpine landscape, mountain
249 soils, and soil organisms.

250 (2) Vegetation

252 Mountain ecosystems above the treeline consist of alpine shrub- and grasslands that gradually give way
253 to high alpine areas extending into the zone of perennial snow and ice. These alpine areas typically have
254 sparse vegetation but often rich cryptogam communities. The treeline itself is a transition zone, a so-called
255 ecotone, between the higher montane forest, often dominated by coniferous trees, and the alpine zone.

256 The abundance of plant species and their distribution are determined by temperature, water availability,
257 and the duration of snow cover, which results from the interacting effects of temperature, precipitation,
258 topography, and wind (Rodwell, 1992a, 1992b; Thompson & Brown, 1992; Panchard *et al.*, 2023). Alpine
259 grasslands share many structural and functional traits and characteristics with polar grass-dominated tundra

260 ecosystems (Riebesell, 1982; Janišová *et al.*, 2011; Dengler *et al.*, 2014), and in both systems, low air- and
261 soil temperatures are an important factor for plant growth. Frost often limits the growth of trees and shrubs
262 (Peel, Finlayson & McMahon, 2007), whereas permafrost (i.e. continuous frost conditions) controls the
263 entire soil system and slows down all biotic activity (Parolo & Rossi, 2008; Zollinger *et al.*, 2013; Goordial
264 *et al.*, 2016; Giaccone *et al.*, 2019; Jin *et al.*, 2020). At the upper limit of grasslands, occasionally increased
265 aridity and shortened vegetation periods cause poikilohydric cryptogamic organisms to gradually replace
266 the standing euryhydric phanerogams (Körner, 2021).

267 Adaptations of alpine vegetation to short and cold growing seasons include the ability to metabolise
268 rapidly at low temperatures, the transition to dormancy as a strategy to withstand the rigours of winter, and
269 the storage of carbohydrates in roots/rhizomes or of lipids in old leaves for regrowth and flower primordia
270 formation (Billings, 1974) (Fig. 2). Alpine plants are also adapted to intense solar radiation, as well as to
271 extended periods of dehydration. Whereas the structure and composition of alpine vegetation depends on
272 soil type and the chemical and physical properties of soil, plant communities, in turn, influence soil
273 structure, properties, and stability.

274 275 276 **IV. CRYPTOGRAMS AND BIOLOGICAL SOIL CRUSTS**

KEY ASPECTS

- Cryptogam communities are widely distributed across different elevational zones in alpine regions
- Biological soil crusts are mainly restricted to high alpine areas.
- Lichen and bryophyte diversity and productivity decline above the treeline towards the nival belt, but at slower rates than that of vascular vegetation.
- The composition of lichen and bryophyte communities is strongly related to bedrock chemistry and soil texture.
- Climate change causes bryophytes to move upwards, whereas at lower elevations sensitive and rare lichens and bryophytes are endangered by vascular plant growth.
- We found 137 publications dealing primarily with alpine cryptogams (i.e. 16 for biological soil crusts and 121 for cryptogams in general), mainly from the mountain regions of Central & Southern Europe (29.9%), Northern Europe (26.3%), and Central Asia (14.6%); see Fig. 1, 3, and Table S4.

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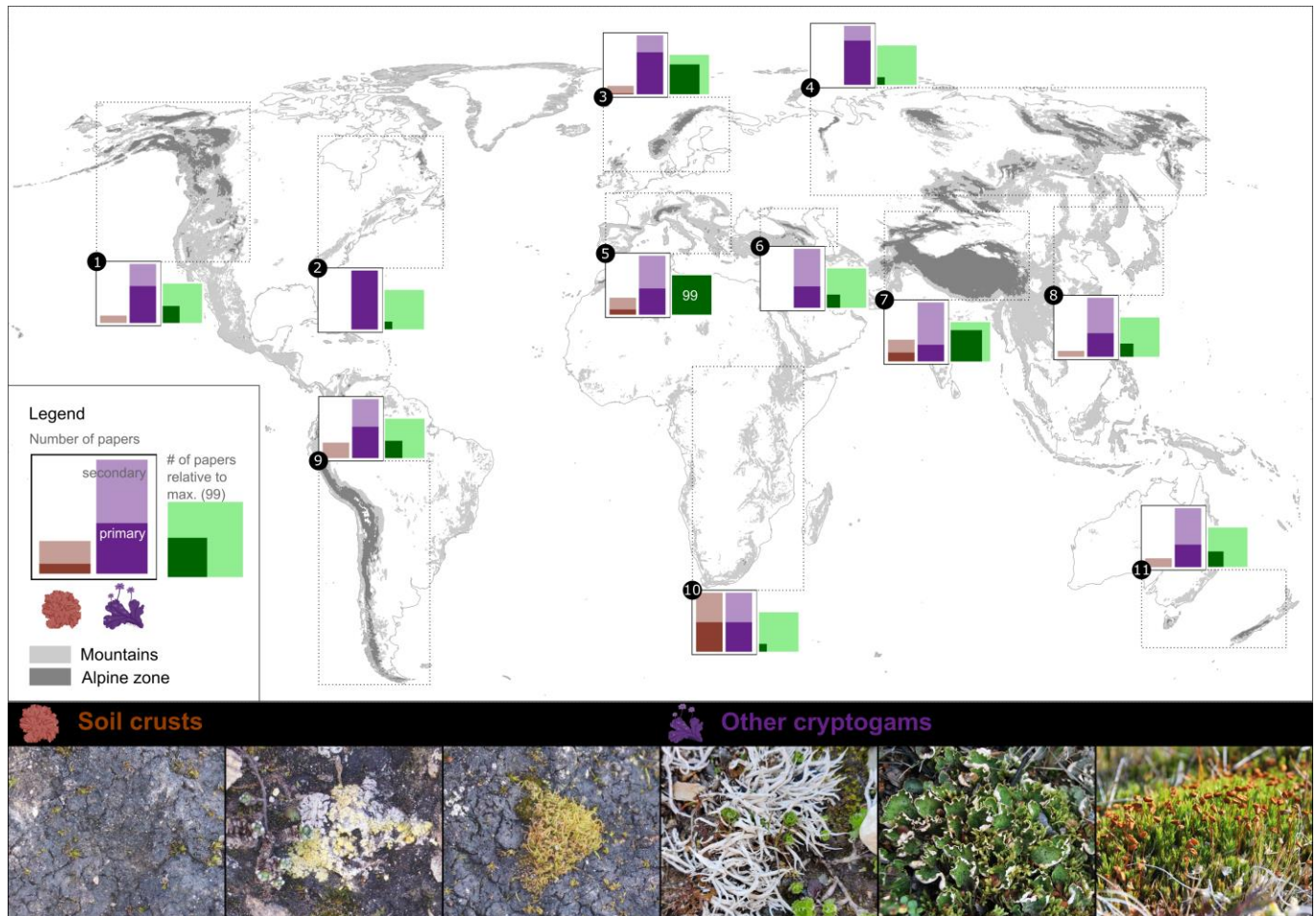


Fig. 3. Global map of available scientific articles focusing on cryptogams in alpine mountain soils. Number of publications is given per crust type and relative to the maximum of papers found (Central & Southern Europe): the dark-coloured part of the bar represents those papers where the organismic group was likely the primary object, the light-coloured part represents those papers where the organismic group was mentioned, but not as the main subject of the publication. See Appendix S1 for a detailed description of the methods and full lists of publication numbers per region and soil organism group. Photos from left to right: Soil crusts: cyanobacteria-dominated soil crust (dark surface colouration) intermingled by bryophytes, in alpine zone of Großglockner, Austria (credit: Stefan Herdy); cyanobacteria-dominated biocrust mixed with chlorolichens, dominated by *Fulgensia* sp., alpine zone of the Großglockner, Austria (credit: Stefan Herdy); cyanobacteria-dominated biocrust mixed with mosses, dominated by *Tortella* sp., alpine zone of the Großglockner, Austria (credit: Stefan Herdy); Other cryptogams: arctic-alpine lichen *Thamnolia vermicularis*, alpine zone of the Großglockner, Austria (credit: Stefan Herdy); arctic-alpine lichen *Peltigera aphosa* in vicinity of Kangerlussuaq, Greenland (credit: Bettina Weber); moss *Polytrichum* sp. in vicinity of Kangerlussuaq, Greenland (credit: Bettina Weber).

294 (1) Cryptogams

295 Cryptogams are non-vascular organisms that do not form flowers and seeds but reproduce by fission,
296 fragmentation, and spores. They comprise lichens, bryophytes, eukaryotic algae, and cyanobacteria (Büdel,
297 Friedl & Beyschlag, 2023). Cryptogams occur widely at different elevations in alpine regions, where they
298 grow epiphytically on vascular plants as well as on and within rocks (saxicolous) and on soil. In some cases,
299 soil-inhabiting (epigaeic) organisms form biological soil crusts (abbreviated as biocrusts). Since biocrusts
300 are defined as an ‘intimate association between soil particles [...] and organisms which live within, or
301 immediately on top of, the uppermost millimetres of the soil’ (Weber *et al.*, 2022), they do not include
302 fruticose lichen and bryophyte carpets, which mainly grow above the soil and form valuable vegetation
303 components on their own. A detailed description of alpine biocrusts is given in Chapter IV.2 below.

304 In Europe, descriptions exist for 200 lichen species in the nival belt of the Alps, with a remarkable
305 development of the genera *Cetraria*, *Parmelia*, and *Umbilicaria* (Ozenda & Borel, 2003). The number of
306 bryophytes and macrolichens increases towards the North, with 439 species of bryophytes in the Italian
307 Alps (Pedrotti & Grafta, 2003), 65 bryophyte and 218 lichen species in the south-eastern Carpathian
308 Mountains (Coldea, 2003), 150–200 species of lichens in the Pyrenees (Gómez, Sesé & Villar, 2003), and
309 about 558 bryophyte species in the Southern and Northern Scandes (Virtanen *et al.*, 2003). Areas with the
310 highest species richness of bryophytes but also the highest numbers of threatened species, are located in the
311 eastern European Alps, Carpathian Mountains, eastern Pyrenees, and the Scandes (Hodgetts *et al.*, 2019).
312 The highest elevational records for lichens and bryophytes are found in the subtropical Dry Andes, near the
313 summit of Socompa volcano at 6,060 m (Halloy, 1991) and on Mount Everest, Himalaya at 7,400 m
314 (*Lecidea vorticosa* (FLÖRKE) KÖRB. and *Pertusaria bryontha* (ACH.) NYL.; (Miehe, 1988).

315 Grassland ecosystems contain a high diversity of cryptogamic autotrophs, especially bryophytes and
316 lichens, whose occurrence is primarily determined by elevation and exposition (Cleavitt, 2004; Daniëls *et*
317 *al.*, 2004; Baniya *et al.*, 2012; Rai, Upreti & Gupta, 2012). Their diversity and productivity follow the
318 same elevational gradients of temperature and aridity as phanerogams (Sundstøl & Odland, 2017); species
319 richness of lichens, bryophytes, and algae increase above the treeline and progressively decline towards the
320 nival belt (Austrheim, 2002; Vittoz *et al.*, 2010).

321 In temperate central European mountains, alpine grasslands are characterised by the presence of large
322 meadows dominated by genera including *Festuca* and *Carex* (Ozenda, 1988), driven by the presence of a
323 long-standing, deep snow cover, which melts relatively fast in spring. In this region, communities
324 dominated by bryophytes and lichens cover only relatively small areas. In contrast, in Central Asian and
325 Scandinavian mountains, higher aridity or a stronger clearing of snow cover by wind promotes communities
326 richer in cryptogams and less dominated by graminoids. This trend is also observed in continental Nearctic
327 mountain ranges such as the Rocky Mountains (Leuschner and Ellenberg 2017). In all mountain ranges,
328 snow abrasion poses a major mechanical challenge to alpine vegetation of exposed habitats (Wieser,

329 Holtmeier & Smith, 2014) and promotes the development of stress tolerant cryptogamic communities in
330 windswept localities.

331 The topographic heterogeneity found in high alpine slopes tends to intersperse grasslands with azonal
332 communities of saxicolous, terricolous, and chasmophytic cryptogams that colonise skeletal soils and
333 patches of exposed mineral substrate. These azonal patches become more abundant towards the nival zone
334 and in arid or windswept localities. There, some fruticose lichens and pleurocarpous mosses grow among
335 graminoid patches and are thereby an integral part of alpine grasslands. The lower dependence of
336 cryptogams on substrate presence can create highly discordant diversity patterns between cryptogams and
337 vascular plants, as well as among cryptogam groups (Di Nuzzo *et al.*, 2021). However, moss and
338 phanerogam richness also showed a strong correlation with soil richness and diversity on the
339 Hardangervidda plateau in Norway (Vestvidda, Southern Scandes), whereas there was no correlation with
340 liverworts (Odland, Reinhardt & Pedersen, 2015). In Palearctic and Nearctic mountains, *Cladonia* species
341 and pleurocarpous mosses such as *Pleurozium* sp. tend to dominate towards the treeline, while cetrarioid
342 species or *Thamnolia* sp. become more common towards the upper part of the gradient.

343 The exact composition of lichen communities varies significantly, depending on the bedrock chemistry
344 and resulting texture of the mineral fraction of local soils (Guo & Cao, 2001). Calcium-rich spring seeps
345 were observed to form a refugium harbouring a rich variety of bryophytes and lichens (Miller, Fryday &
346 Hinds, 2005). Conversely, areas with higher water retention and permanently flooded soils develop into
347 bryophyte dominated bogs mostly shaped by *Sphagnum* species and pleurocarpous mosses (Halsey, Vitt &
348 Gignac, 2000; Wahren, Williams & Papst, 2001; Bragazza, Gerdol & Rydin, 2003). Also in wetlands,
349 fens, springs, and snowfields, cryptogams can reach high diversity (Dierssen & Dierssen, 2005; Cooper *et*
350 *al.*, 2010; Austin & Cooper, 2016). In alpine fellfields, cryptogams are a prominent component, with
351 lichens covering up to about 50% of the surface area on the Beartooth Plateau, Montana and Wyoming
352 (Greater Yellowstone Rockies; Eversman, 1995). Generally, lichen communities develop on substrates
353 with little mechanical perturbation under changing hydration conditions. Wet and soft soils of glacier
354 forefields are not colonised by lichens. Soils in many windswept localities are typically colonised by
355 fruticose lichens, which usually interlock with shrubby plants rather than being connected with the soil. In
356 contrast to a common notion of lichens as pioneer vegetation, crustose lichens in biocrust communities need
357 not only soil stability but also long stable time intervals to develop, and they can suffer extinction due to
358 shading from nearby plants. One means by which evolution has made it possible for lichens to overcome
359 competition with plants or unsuitable soil conditions is by the development of shrublike fruticose
360 morphologies, which grow as lichen heath and pleurocarpous mosses between persistent plant vegetation
361 such as dwarf shrubs (e.g. genera *Vaccinium*, *Salix*, and *Erica* with *Hypnum cupressiforme* HEDW.;
362 Schellenberg & Bergmeier, 2020).

363 Compared to phanerogams, which show high levels of endemism, lichens associated with alpine
364 grasslands have very broad distributions, often being apparently sub-cosmopolitan. This interregional
365 connectivity in arctic-alpine organisms has been studied in lichens (Fernández-Mendoza & Printzen, 2013;
366 Garrido-Benavent & Pérez-Ortega, 2017; Onuț-Brännström, Tibell & Johannesson, 2017), but also occurs
367 in bryophytes (Mirek & Piekos-Mirkowa, 1992), and seems to reflect range expansions originating from
368 interregional connectivity during the Pleistocene. This does not exclude the rare endemism of lichens at
369 higher elevations, which can be due to substrate conditions that are not or hardly found elsewhere, or to
370 habitat shrinkage due to climatic factors (e.g. *Cetradonia linearis* (A.EVANS) J.C.WEI & AHTI is only found
371 in few localities in the Appalachian Mountains; Woodward, 2021).

372 While soil properties are key in determining cryptogam presence and composition, effects are reciprocal,
373 and cryptogams also influence soil properties. For example, in an alpine *Vaccinium* thicket accompanied
374 by *Polytrichum strictum* MENZIES EX BRIDEL and *Sphagnum* sp., the moss cover caused a pedogenic
375 feedback by increased water storage, which promoted stronger weathering and increased dissolved organic
376 C contents in the soil. The latter then caused the soil to cross the threshold of podsolisation (Musielok *et*
377 *al.*, 2021). Similarly, mat-forming lichens have also been shown to influence litter decomposition and
378 buffer soil temperatures in subalpine and alpine environments (van Zuijlen *et al.*, 2020; Mallen-Cooper,
379 Graae & Cornwell, 2021). Mosses, in turn, have been reported to mediate soil properties such as
380 temperature, moisture, and C:N ratios, with varying effects depending on the shrub species under which
381 they occur (Bueno *et al.*, 2016). Generally, lichens and mosses also contribute to soil stability and reduce
382 erosion in alpine environments (Martin *et al.*, 2010).

383 The interactions between plants and lichens have also been explored (Favero-Longo & Piervittori,
384 2010). Most notably, the elimination of fruticose lichens, especially cetrarioid species, has been shown to
385 significantly reduce the growth of neighbouring grasses and sedges (Jespersen, 2013), probably as a result
386 of changes in microclimate, surface water retention, and protection from run-off. In an experimental
387 approach, presence of most lichens facilitated seedling recruitment, while only very thick mats of *Cladonia*
388 *stellaris* (OPIZ) POUZAR & VĚZDA had an inhibitory effect (Nystuen *et al.*, 2019). Interactions between
389 vascular plants and bryophytes are also variable. *Ptilium crista-castrensis* DE NOTARIS, a feather moss, was
390 observed to have a negative effect on the survival of alpine tree seedlings, likely due to altered competition
391 or nutrient availability, whereas *Sphagnum* mosses had no effect (Lett *et al.*, 2020). In contrast, a study in
392 a boreal forest-tundra ecotone (Central Labrador Ranges, Canada) revealed that a *Pleurozium schreberi*
393 MITTEN seedbed improved seed emergence, survival, and nutrient availability for black spruce (Wheeler,
394 Hermanutz & Marino, 2011). Similarly, *Racomitrium lanuginosum* BRIDEL, mats stimulated growth of the
395 sedge *Carex bigelowii* TORR. EX SCHWEIN. in the alpine/subarctic tundra of Swedish Lapland (Carlsson &
396 Callaghan, 1991).

397 Effects of environmental changes on cryptogams are likely diverse. Climate change in alpine regions
398 generally causes a shift of bryophytes to higher elevations (Wen *et al.*, 2022), whereas nutrient input, CO₂
399 increase, or warming, cause vascular plant productivity to increase at the cost of sensitive and long-
400 established soil lichen and bryophyte communities (Graglia *et al.*, 2001; Klanderud, 2008; Dawes *et al.*,
401 2017). Such changes in plant communities also affect microbial community composition, which may result
402 in altered biogeochemical cycling (Bueno de Mesquita *et al.*, 2017).

403 Anthropogenic drivers, such as grazing, trampling, and N deposition also affect cryptogams in complex
404 and multiple ways. For instance, the effects of grazing are variable. Grazing in extensively farmed
405 secondary grasslands has been shown to increase the diversity and coverage of bryophytes and lichens due
406 to a decreased competition for light (Nascimbene, Fontana & Spitale, 2014). On the other hand, in mid-
407 elevation pastures in India (3000–3400 m), where significant grazing by cattle occurs, lichen diversity is
408 reduced compared to higher (3400–4000 m) and lower (2700–3000 m) habitats (Rai *et al.*, 2012). In the
409 Uinta Mountains of Utah (Western Rocky Mountains), grazing favoured the growth of crustose or
410 squamulose lichens, whereas in ungrazed areas fruticose and foliose taxa also occurred (St. Clair *et al.*,
411 2007). Vascular plants are also influenced, since further effects of (heavy) grazing include an increase in
412 root biomass (Mayel, Jarrah & Kuka, 2021), also in alpine meadows (Yang *et al.*, 2018), likely resulting
413 from increased rates of nutrient cycling due to herbivore excretion. The effects of human trampling include
414 the reduction of lichen abundance and diversity in an alpine heath ecosystem in northern Sweden
415 (Jägerbrand & Alatalo, 2015) as well as a reduced coverage of the moss *Pleurozium schreberi* (WILLD. EX
416 BRID.) MITT. in a subarctic grassland (Sørensen *et al.*, 2009).

417 Finally, existing evidence for the effects of N deposition on cryptogams includes a loss in moss cover in
418 an alpine *Racomitrium* moss-sedge heath in the United Kingdom (Britton *et al.*, 2018), a general decline in
419 richness, and a community shift from bryophytes and lichens towards graminoids (Nilsson *et al.*, 2002;
420 Armitage *et al.*, 2014; Britton *et al.*, 2019). Declines in moss cover are possibly due to the positive effects
421 of N deposition on the growth of moss-associated fungi (Taylor *et al.*, 2022). In a study in Norway, N
422 addition caused a decrease in lichen cover and size (Fremstad, Paal & Mols, 2005), whereas in northern
423 Sweden, N, P, and K fertilisation positively affected bryophyte biomass (Haugwitz & Michelsen, 2011).

424 After disturbance, succession under natural conditions or facilitated by restoration measures may help
425 to reach the natural vegetation state again. In a study investigating the succession on alpine soil heaps in
426 western Norway, it took about 30 years until the bryophyte and lichen cover and species richness was
427 similar to the surrounding area (Rydgren *et al.*, 2011). Similar results were also obtained in a separate study,
428 where gamma diversity of cryptogams peaked 23 to 28 years after cessation of ploughing and fertilising
429 subalpine grasslands (Austrheim & Olsson, 1999). In a study on habitat restoration after clearcutting of
430 non-indigenous *Pinus mugo* TURRA in the Eastern Sudetes (Bohemian Massif), bryophyte diversity was
431 mapped and compared to that in areas of undisturbed dwarf pine canopy and in autochthonous grassland

432 areas. The results revealed a habitat homogenisation, as related to bryophytes, nine years after the impact,
433 and suggested that restoration measures, in addition to clear-cutting, might be helpful to enhance restoration
434 speed and quality (Zeidler *et al.*, 2022). In a different study in Iceland, application of shredded turf led to a
435 quick increase in bryophyte cover and thus might form a valuable restoration measure (Aradottir, 2012).

437 (2) Biocrusts

438 As a pioneer community in alpine environments, biological soil crusts (biocrusts) comprise a dense layer
439 of cyanobacteria, green algae, lichens, and bryophytes that covers the soil surface (Gold, Glew & Dickson,
440 2001; Huber *et al.*, 2007; Karsten & Holzinger, 2014; Mikhailiyuk *et al.*, 2015; Weber, Büdel & Belnap,
441 2016) and grows in patches between vascular plants (Türk & Gärtner, 2003). Unlike lichen and bryophyte
442 carpets, biocrusts do not elevate much above the soil surface. However, their presence and activity play a
443 crucial role in forming soil aggregates, thereby enhancing soil stability. Early successional communities
444 are dominated by cyanobacteria, which facilitate the gradual colonisation by lichens and bryophytes under
445 suitable conditions. A more detailed definition of biocrusts and their delimitation against other cryptogam
446 communities was published by Weber *et al.* (2022). Whereas cryptogams occur widely in alpine grasslands,
447 biocrusts are mainly restricted to the high alpine zone, where they can achieve very large cover values. In
448 the Austrian Alps (Hochtor, High Tauern), for example, biocrust coverage reached up to 30% of the surface
449 area in the studied homogeneous vegetation unit (Büdel *et al.*, 2014), with a high prevalence of
450 cyanobacteria, which has also been observed in Himalayan soils (Reháková, Chlumská & Doležal, 2011).
451 An increase with elevation was also detected for cyanobacterial biomass in cyanobacteria-dominated
452 biocrusts in the Zanskar Range (Himalaya; Janatková *et al.*, 2013).

453 The occurrence and composition of biocrusts in alpine regions appear to be mainly influenced by habitat
454 availability and precipitation (Büdel *et al.*, 2009; Lütz, 2012; Jung *et al.*, 2018; Xiao *et al.*, 2020). Biocrust
455 activity status, in turn, is regulated by morphological, physiological, and local microclimatic conditions
456 (Longton, 1988; Tamm *et al.*, 2018). Additional variables affecting biocrust occurrence include elevation,
457 aspect, snowpack, dust input in alpine areas, as well as standing vegetation (Miller, 2009; Sun *et al.*, 2013;
458 Mejia *et al.*, 2020; Peer *et al.*, 2022). Across four mountain ranges at high elevation in Ladakh, India,
459 cyanobacterial occurrence along an elevational gradient from 3,700–5,970 m was mainly determined by
460 the studied mountain range, but also elevation and vegetation type were relevant (Reháková *et al.*, 2011).
461 Whereas *Oscillatoriales* mostly occurred on alpine meadows, *Nostocales* were dominant in the subnival
462 zone and screes.

463 Thawing of permafrost and glaciers produce particularly suitable habitats for biocrusts. Accordingly,
464 apart from long-established cryptogam communities, (cyano-)bacteria, (lichenised) fungi, and algae play a
465 key role in primary substrate colonisation after glacier retreat. This has been investigated in different alpine
466 regions around the world, including Norway, Chile, Peru, and in the European Alps (Frey *et al.*, 2013;

467 Bilovitz *et al.*, 2014b; Matthews & Vater, 2015; Krisai-Greilhuber *et al.*, 2017). In Tierra del Fuego, Chile
468 (Cordillera Darwin, Patagonian Andes), bacterial communities with cyanobacteria and algae of the order
469 *Prasiolales* were the dominating groups close to the glacier terminus, whereas lichen-forming and parasitic
470 fungi occurred in early successional stages (Fernández-Martínez *et al.*, 2017). Cyanobacteria hosted by
471 bryophytes and fertilising the immature soils by actively fixing atmospheric N were also observed 4–7
472 years after deglaciation (Arróniz-Crespo *et al.*, 2014). Cyanobacteria were further described to play a vital
473 role in primary succession with respect to both C and N fixation and soil stabilisation at high elevations
474 (5,000 m) in the Cordillera de Vilcanota (Cordillera Oriental, Peru) (Schmidt *et al.*, 2008). In the case of
475 lichens, multiple studies in the European Alps describe an increasing abundance and diversity with moraine
476 age (e.g. Bilovitz *et al.*, 2014b, 2014a, 2015) and higher coverage compared to the surrounding non-
477 glaciated area (Hestmark, Skogesal & Skullerud, 2007). In central Svalbard, repeated surveys of glacier
478 forefields 10–20, 30–50, and 80–100 years after glaciation detected a marked shift in cryptogam community
479 structure over time (Pessi *et al.*, 2019).

480 Biocrusts provide ecosystem services via their functions in soil stabilisation, N and C fixation, nutrient
481 accumulation, and water retention (Gold *et al.*, 2001; Huber *et al.*, 2007; Peer, 2010; Zheng *et al.*, 2014;
482 Jung *et al.*, 2018; Borchhardt *et al.*, 2019). They are further known for improving soil microenvironments,
483 mainly due to the activity of microorganisms within the biocrust (Wei *et al.*, 2022). In the case of glacier
484 forefields, cyanobacteria fix and thus provide N to the strongly N-limited raw soils, with rates directly
485 related to the availability of organic C (Wang *et al.*, 2021). High N fixation rates by alpine *Collema*-
486 dominated biocrusts in the mountains of Western Canada (i.e. Chilcotin Plateau (British Columbia Interior)
487 and Southern Icefield Ranges (Saint Elias Mountains)) suggest an important contribution of cyanolichens
488 to ecosystem N budgets (Marsh *et al.*, 2006). While Antarctic and alpine biocrusts show similarities in
489 composition, alpine biocrusts seem to be much more physiologically active than their polar counterparts
490 (Colesie *et al.*, 2014, 2016), with activity rates closely linked to the local climatic conditions (Raggio *et al.*,
491 2017).

492 An additional effect of biocrusts is their influence on soil temperature. This was shown for instance on
493 the Tibetan Plateau, where Ming *et al.* (2022) found that at a depth of 5 to 100 cm, soil temperatures were
494 0.6–1.0 °C lower in the presence of biocrusts; Xu *et al.* (2020) showed similar effects for moss-dominated
495 biocrusts. These results differ from previous studies, where biocrusts increased surface temperatures due to
496 their dark colour (Chamizo *et al.*, 2013). A possible explanation is the high insulating potential of soil
497 organic matter and the high water-holding capacity of the local biocrusts (Ming *et al.*, 2022). Biocrusts on
498 the Tibetan Plateau (i.e. Min Mountains and Qilian Mountains), were also observed to significantly reduce
499 soil pH in the upper 10 cm (Xu *et al.*, 2020) and to impact seed germination, thus influencing vascular plant
500 community composition (Li *et al.*, 2016). In another study, biocrusts tended to support the survival of

501 *Nothofagus pumilio* (POEPP. & ENDL.) KRASSER tree seedlings in the southern Patagonian Andes (Pissolito,
502 Garibotti & Villalba, 2021).

503 Besides their effects on environmental conditions, biocrusts also comprise various bacterial
504 communities. Bacterial composition within biocrusts appears to be strongly impacted by the dominating
505 photoautotrophs (i.e. cyanobacteria, algae, lichens, or bryophytes), whereas for microfungi such a link
506 could not be observed (Maier *et al.*, 2018; Abed *et al.*, 2019). Along an aridity gradient on the Tibetan
507 Plateau, algae-dominated biocrusts hosted more diverse bacterial communities, with diversity increasing
508 with rising aridity, while in lichen-dominated biocrusts bacterial communities were less diverse and
509 bacterial diversity decreased with rising aridity. Whereas the bacterial communities differed depending on
510 the biocrust type, they were also influenced by environmental and stochastic processes (Wei *et al.*, 2022).
511 In alpine biocrusts, the soil–lichen interface was colonised by characteristic bacteria, namely
512 Alphaproteobacteriota and Acidobacteriota (Muggia *et al.*, 2013).

513 Adaptive strategies of lichens to severe conditions in alpine regions include accumulation of UV-
514 absorbing phenolic usnic acid and storage of polyols for protection of cellular constituents during
515 desiccation (Bligny & Aubert, 2012; Armstrong, 2017). Protective strategies of terrestrial, photosynthetic
516 green algae include photoprotection, non-photochemical quenching and flexibility of secondary cell walls
517 (Karsten & Holzinger, 2014; Kitzing, Pröschold & Karsten, 2014). Diurnal freeze–thaw cycles that
518 frequently occur in high alpine habitats were shown to have no negative impact on the growth of
519 cyanobacteria-dominated biocrusts collected in the Peruvian mountains of the Cordillera Oriental (Schmidt
520 & Vimercati, 2019).

521 Land use by agriculture and recreational activities can cause severe damage to high-mountain
522 ecosystems, including their biocrusts. On high elevational grasslands of the Ötztal Alps (European Alps) in
523 Tyrol, Austria, for example, even weak trampling pressure caused a decrease in the frequency of sensitive
524 species, including fruticose and crustose lichens (Grabherr, 1982). Also, in the Canadian Rockies of
525 Alberta, recreational trails had substantially lower coverage of lichens and biocrusts, as compared to
526 undisturbed sites (Crisfield, Macdonald & Gould, 2012). After disturbance of biocrusts in alpine habitats,
527 restoration could be facilitated by inoculation with mature biocrusts (Letendre, Coxson & Stewart, 2019).
528 Climate change poses another threat: In Switzerland, the observed increase in the mean elevation of
529 bryophytes, driven by extinction of cryophilous species at lower elevations and by an upward movement at
530 their upper range limits, was likely a result of recent climate change (Bergamini, Ungricht & Hofmann,
531 2009). Changes in bryophyte and lichen species richness, cover, and composition were also observed during
532 a 15-year period from 2001 and 2015 in the Southern Scandes of Norway, with an effect on species
533 interactions. For lichens, the observed decrease in species richness and cover over time was attributed to
534 the increased competition with vascular plants (Vanneste *et al.*, 2017).

536

V. SOIL MICROBIOTA

KEY ASPECTS

- Soil microorganisms are essential for mineralization processes, nutrient cycling and for many symbiotic relationships with plants and animals.
- The very great majority of soil microorganisms cannot be investigated by culture-based approaches that, therefore, need to be further improved.
- Knowledge about the enormous microbial diversity in alpine soils is distinctly increasing since the advent of high-throughput molecular methods.
- Microbial diversity is determined by complex interactions with abiotic soil properties such as soil pH, water content and quality and quantity of organic matter.
- Changes in microbial communities can have cascading effects on other components of the ecosystem.
- Fungal diversity is more strongly influenced by plants than the diversity of prokaryotes.
- Patterns of diversity and effects of abiotic and biotic drivers are distinctly group specific.
- We found 412 publications dealing primarily with alpine microbial soil diversity (i.e. 16 for archaea, 190 for bacteria, 184 for fungi, and 23 for protists), mainly from the mountain regions of Central Asia (50.7%), Central & Southern Europe (25.0%), and the North American Cordillera (6.8%); see Fig. 4 and Table S5.

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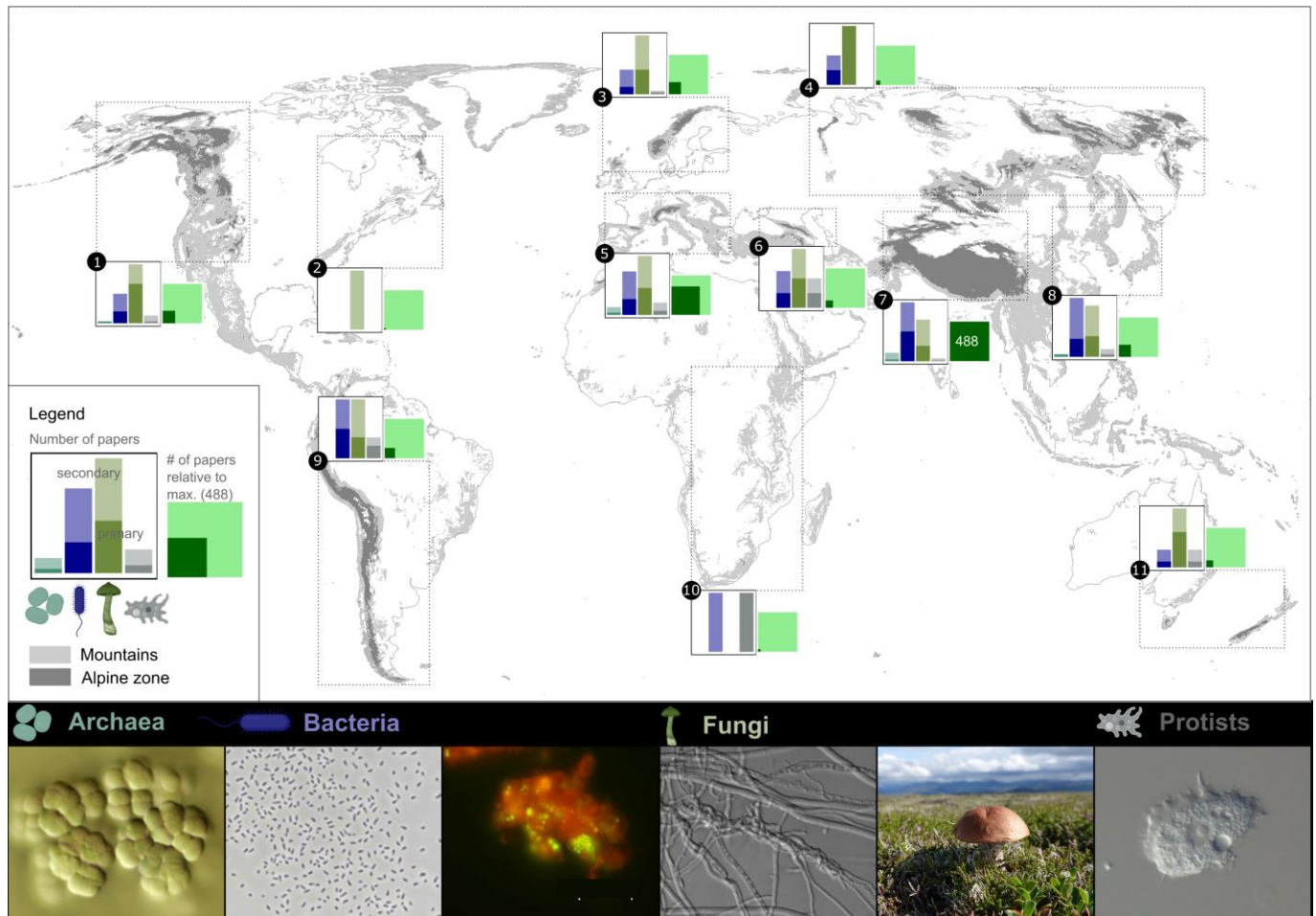


Fig. 4. Global map of available scientific articles focusing on microbial diversity in alpine mountain soils. Number of publications are given per microbial group and relative to the maximum of papers found (Central Asia): the dark-coloured part of the bar represents those papers where the organismic group was likely the primary object, the light-coloured part represents those papers where the organismic group was mentioned, but not as the main subject of the publication. See Appendix S1 for a detailed description of the methods and full lists of publication numbers per region and soil organism group. Photos from left to right: Archaea: *Methanosarcina* sp. (credit: Paul Illmer), Bacteria: *Methylosinus sporium* (credit: Nadine Praeg), DNA (green) stained microscope preparation of soil bacteria attached to soil particle (red) (credit: Nadine Praeg & Paul Illmer), Fungi: *Trichoderma asperellum* intercoiled with *Botrytis* sp. (credit: Siebe Pierson), *Leccinum vulpinum* (credit: Andrea J. Britton), Protists: *Acanthamoeba* sp. (credit: Kenneth Dumack).

(1) Bacteria and Archaea (Prokaryotes)

Prokaryotes include two distinct phylogenetic domains, archaea and bacteria, which are both characterised by the absence of a cell nucleus. Most prokaryotes are unicellular and reproduce asexually. Due to a very high metabolic diversity (various chemo- and phototrophic ways of life), prokaryotes colonise almost every ecological niche on Earth.

559 A significant proportion of prokaryote diversity studies on high alpine soils (King *et al.*, 2010; Yashiro *et al.*, 2016) and alpine permafrost have been conducted on the Tibetan Plateau in Central Asia, which
560 harbours the largest area of mountain permafrost soils globally (Cheng *et al.*, 2022), resulting in 54 % of
561 all prokaryote diversity studies in mountain soils being performed in Central Asia (Fig. 4). Studies
562 addressing microbial diversity (all prokaryotes, selected studies also including fungi and protists) in
563 mountain permafrost outside of China were conducted recently in the European Alps (Frey *et al.*, 2016;
564 Luláková *et al.*, 2019; Praeg, Pauli & Illmer, 2019; Adamczyk, Rüthi & Frey, 2021; Sannino *et al.*, 2021)
565 and high-elevation soils from the Andes, Rocky Mountains, and Alaskan Brooks Range (Lipson &
566 Schmidt, 2004; Nemergut *et al.*, 2005; King *et al.*, 2010; Ricketts *et al.*, 2016; Wagner *et al.*, 2017; Farrer
567 *et al.*, 2019). Despite partially harsh environmental conditions, mountain soils harbour a considerable
568 bacterial diversity (Rime *et al.*, 2015; Frey *et al.*, 2016). Bacteria contribute substantially to
569 biogeochemical cycles, both at the regional and supraregional scale (Donhauser & Frey, 2018) and together
570 with archaea (and fungi, see Section V.2) are considered fundamental in stabilising soils and influencing
571 the physical and biological development of soil ecosystems (Bernasconi *et al.*, 2011). Prokaryotic
572 colonisers contribute significantly to the initial build-up of biomass, by fixation of atmospheric CO₂ and
573 N₂ (Frey *et al.*, 2013), and using C and N from (microbial) necromass (Zumsteg, Schmutz & Frey, 2013b;
574 Rime *et al.*, 2016b; Donhauser *et al.*, 2021). Quantification of precise amounts of CO₂ and N₂ fixation and
575 usage of dead microbial cells as a non-negligible C pool in mountain soils is challenging due to the
576 complexity and variability of mountain soils and is still lacking. Further nutrients, such as P and S, may be
577 obtained from the bedrock by biological weathering (Frey *et al.*, 2010; Brunner *et al.*, 2011). As glaciers
578 increasingly retreat with climate change, barren bedrock is exposed and colonised by pioneer
579 microorganisms such as Acidobacteriota, Planctomycetota and Bacteroidota (Zumsteg *et al.*, 2012; Rime
580 *et al.*, 2015; Rime, Hartmann & Frey, 2016a). From permafrost soils, bacterial candidate phyla OD1, TM7,
581 GN02 and OP11 forming the superphylum Patescibacteria were recovered besides well-established phyla,
582 such as Proteobacteria, Verrucomicrobiota and Acidobacteriota and were found to represent one third of
583 the entire community (Frey *et al.*, 2016). At lower elevations, e.g. in alpine grasslands, bacterial
584 communities are primarily dominated by Acidobacteriota (subgroup6, Acidobacteria), Actinobacteriota
585 (Actinobacteria, Thermoleophilia), Proteobacteria (Alpha- and Gammaproteobacteria), Bacteroidota
586 (Bacteroidia), and Verrucomicrobiota (Yuan *et al.*, 2014, 2015; Yashiro *et al.*, 2016; Chen *et al.*, 2020,
587 2021; Ji *et al.*, 2020). Gemmatimonadota and Bacillota (formerly Firmicutes) are further phyla that are
588 commonly present in alpine grasslands, such as in the Tibetan Plateau (Jiang *et al.*, 2021). Studies
589 specifically addressing archaeal communities in grasslands are still lacking. However, existing work
590 suggests that Thaumarchaeota (Nitrosphaeria), Nanoarchaeota (Woesearchaeota), Crenarchaeota
591 (Bathyarchaeota, Thermoprotei), and Euryarchaeota (Thermoplasmata, Methanobacteria) represent the
592 most prevalent archaeal phyla (Malard *et al.*, 2022). However, ongoing changes in microbial taxonomy, for
593

594 archaea (and bacteria), facilitated by the widespread availability of genome sequences that led to the
595 development of comprehensive sequence-based taxonomies like the Genome Taxonomy Database (GTDB)
596 (Parks *et al.*, 2018) should be considered. Besides, the coverage of archaea can be less than 25% by using
597 universal primers for 16S metabarcoding (Bahram *et al.*, 2019) and selective and specific detection of
598 archaea has been rarely done so far and is thus urgently needed. The dominance of Actinobacteriota and
599 Acidobacteriota and especially of ammonium-oxidising archaea is due to their adaptation to the N- and P-
600 limited conditions typical for alpine grassland soils or higher elevation soils (Liu *et al.*, 2017; Ma *et al.*,
601 2019; Praeg *et al.*, 2019).

602 Wang *et al.* (2015) reported no clear trend across a transect spanning 3,106 to 4,479 m on Mount Shegyala
603 (Transhimalaya), Tibetan Plateau in the abundances of bacteria and archaea; however, they found that the
604 ratio of bacterial to archaeal gene copy numbers (as a function of abundances) decreased with increasing
605 elevation, highlighting a switch in favour of archaea. Liang *et al.* (2023) compared variations in taxonomic
606 and functional (N cycle) dis/similarity of bacteria across the Tibetan plateau and found that both were more
607 driven by soil abiotic characteristics than vegetation, but with different environmental drivers prevailing
608 for each. Lazzaro *et al.* (2015) observed the lowest bacterial and fungal abundances at the highest site of an
609 elevational transect in the Swiss Uri Alps (1,930–2,519 m, European Alps). Similar to findings for
610 phylogenetic marker genes, functional gene abundance and diversity were shown to vary with elevation in
611 these studies. Yang *et al.* (2014), in turn, studied the functional diversity at four sites along an elevational
612 gradient in the Qilian Mountains (Tibetan Plateau). Abundance of the Rubisco (ribulose-1,5-bisphosphate
613 carboxylase/oxygenase, involved in CO₂-fixation) gene was lower at the lowest site compared to the other
614 sites, which might indicate lower CO₂-fixation activities (Yang *et al.*, 2014; Guo *et al.*, 2015). A succession
615 of the functional genetic potential has also been demonstrated in Swiss glacier forefields (Feng *et al.*, 2023).

616 Given that the majority (approximately 99%) is not cultivable, high-throughput sequencing (HTS) has
617 become a powerful tool for assessing and comparing the diversity of prokaryotes, and metagenome
618 assembled genomes increasingly help to describe the uncultivable majority (Hug *et al.*, 2016). In alpine
619 systems, the composition, distribution, and structure of microbial communities depend on a number of
620 environmental factors such as temperature, precipitation, and other climatic variables such as moisture and
621 snow cover duration (Malard *et al.*, 2022), substrate and nutrient availability, biotic interactions, slope
622 aspect (Adamczyk *et al.*, 2019), as well as soil physicochemical and vegetation properties (Shen *et al.*,
623 2015; Donhauser & Frey, 2018; Adamczyk *et al.*, 2019; Praeg *et al.*, 2019, 2020; Liang *et al.*, 2023).

624 While temperature and precipitation typically have a direct effect on microbial communities, the effects of
625 soil and vegetation properties are likely indirect and depend on climatic variables as well as biological and
626 chemical feedback. Yet, the establishment of plants has been identified as an important driver of prokaryotic
627 community structure during early succession (Rime *et al.*, 2015; Wojcik *et al.*, 2020). Overall, edaphic
628 factors such as soil pH, organic matter content, water, and available P concentrations (Yashiro *et al.*, 2016;

629 Bueno de Mesquita *et al.*, 2020) remain the main determinants of bacterial and archaeal richness, diversity,
630 and community composition. Soil transplantation experiments to study the changes in the taxonomic and
631 functional gene structures of microbial communities with warming (Zumsteg *et al.*, 2013a; Rui *et al.*, 2015)
632 confirm field observations. In these studies, changes in the structure of the community were attributed to
633 temperature, moisture, soil properties, and vegetation parameters. By condensing information on
634 community composition to microbial richness and diversity indices, it was shown that bacterial richness
635 decreased with increasing elevation (Shen *et al.*, 2015; Adamczyk *et al.*, 2019; Praeg *et al.*, 2019), whereas
636 for archaea, Singh *et al.* (2012) documented a peak in alpha-diversity at mid-elevations along a 1,000–3,760
637 m gradient on Mount Fuji (Kantō Mountains), Japan. In glacier forefield soils, microbial community
638 composition was reported to shift in response to increasing C content in soils, decreasing soil pH, and plant
639 establishment (Zumsteg *et al.*, 2012). Temperature further affects microbial communities when it reaches
640 extremes (>25 °C) and passes a tipping point where microorganisms react to further temperature increase
641 with pronounced non-linear responses in community-level growth rates, changes in the temperature
642 sensitivity of bacterial growth (Q10), and alterations in community structure (Donhauser *et al.*, 2020,
643 2021). While fungal communities are tightly associated with plants (see Section V.2), bacterial and archaeal
644 communities are also influenced by other prokaryote communities (Malard *et al.*, 2022). Soil functions and
645 processes are driven by microbial interactions, and the study of network interactions among bacterial,
646 archaeal, and fungal microbiota is gaining interest. In alpine grasslands, soil pH was found to be a key
647 driver for predicting network-level topological features of soil microbial co-occurrence networks; with
648 increasing soil pH, associations between microorganisms were enhanced and networks became more stable
649 (Chen *et al.*, 2021).

650 Overall, central gaps in knowledge about prokaryotic diversity in alpine soil exist, firstly, in a
651 geographical context. Considering the data from Fig. 4, it is obvious that the global distribution of microbial
652 studies is heterogeneous. Secondly, a deficit we observe is the lack of knowledge about the activity and
653 ecological functions of prokaryotes in situ. While molecular data provide information about phylogeny,
654 conclusions about the function of specific clades are often drawn from few cultured isolates which may not
655 be representative for the entire group (e.g. Verrucomicrobiota). Furthermore, there is a growing need to
656 increasingly take into account the complex interactions among microorganisms themselves, as well as their
657 relationships with plants and soil organisms, when investigating and evaluating microbial diversity.

658

659 (2) Fungi

660 Fungi comprise a large ecologically heterogenous group of microorganisms (Stajich *et al.*, 2009), of
661 which only 2–6% of the estimated 1.5–12 million species have been formally described (Taylor *et al.*, 2014;
662 Hawksworth & Lücking, 2017; Bhunjun *et al.*, 2022). Functionally, fungi range from ecosystem recyclers,
663 as the main saprotrophic decomposers of (recalcitrant) organic materials (Baldrian & Valášková, 2008;

664 Finlay & Thorn, 2019), to those forming a great diversity of symbiotic associations with plants and animals
665 (Mueller & Gerardo, 2002; Crowther, Boddy & Hefin Jones, 2012; Genre *et al.*, 2020). It is this
666 multifunctionality that makes fungi essential components of soil biodiversity in all terrestrial habitats
667 (Wagg *et al.*, 2014), including high alpine ecosystems.

668 To date, much of what is known concerning alpine soil fungal communities comes from European and
669 North American studies of the macroscopic reproductive structures (the sporocarps) produced by fungi.
670 Studies include taxonomic works (Horak, 1993; Cripps, Larsson & Horak, 2010), community and
671 biogeographic studies (Senn-Irlet, 1988, 1993; Ronikier, 2008), and ecological investigations (Graf, 1994).
672 These studies have identified a rich diversity of saprotrophic and plant associated symbionts, many of which
673 appear to be restricted to alpine and arctic environments (Cripps *et al.*, 2019).

674 There are comparably few metabarcoding studies that have included analyses of whole fungal
675 communities in alpine soils, although elevational gradient studies often comprise samples from vegetation
676 neighbouring high-elevation treelines, including alpine heaths (e.g. Tonjer *et al.*, 2021). Alpine grassland
677 fungal communities have been investigated using metabarcoding approaches in China (Yang *et al.*, 2017;
678 Jiang *et al.*, 2018; Zhang *et al.*, 2020; Zhang & Fu, 2021) and Central Europe (e.g. Pellissier *et al.*, 2014;
679 Praeg *et al.*, 2019), regions which comprise 79% of the fungal diversity studies found (Fig. 4). These studies
680 demonstrate that different functional groups show a range of responses to changes in elevation, temperature,
681 N addition, and grazing management. In the European Alps, fungi are locally diverse (Brunner *et al.*, 2017;
682 Adamczyk *et al.*, 2019; Praeg *et al.*, 2019; Arraiano-Castilho *et al.*, 2021), similar to other alpine regions
683 (Bjorbækmo *et al.*, 2010; Perez-Mon, Frey & Frossard, 2020; R  thi *et al.*, 2020). In alpine grassland, soil
684 fungal communities are primarily composed of Ascomycota and Basidiomycota, but also comprise large
685 proportions of unidentified fungi (Pellissier *et al.*, 2014; Malard & Pearce, 2018; Praeg *et al.*, 2020).
686 Within these phyla, Agaricomycetes (Basidiomycota), Archaeorhizomycetes (Ascomycota),
687 Sordariomycetes (Ascomycota) and Leotiomycetes (Ascomycota) are the most abundant classes of fungi
688 in grasslands (Pellissier *et al.*, 2014; Pinto-Figueroa *et al.*, 2019). Agaricomycetes are commonly
689 saprotrophic (decomposers) and actively participate in the decomposition of organic matter (Ludley &
690 Robinson, 2008; Edwards & Zak, 2010), especially in cold and dry environments (Ludley & Robinson,
691 2008). Sordariomycetes and Leotiomycetes are ecologically diverse and include pathogens of either plants
692 and animals, mycorrhiza and plant endophytes, as well as saprotrophs (Maharachchikumbura *et al.*, 2016;
693 Johnston *et al.*, 2019). Finally, the Archaeorhizomycetes are a widely distributed and abundant class of
694 terrestrial fungi, yet, their role in the ecosystem is still debated (Rosling, Timling & Taylor, 2013;
695 Pinto-Figueroa *et al.*, 2019) and their detection is hampered by using the ITS2 region instead of the 18S
696 rRNA gene (Tonjer *et al.*, 2021). Archaeorhizomycetes are believed to be associated with plant roots, but
697 experiments suggest they are neither mycorrhizal nor pathogenic (Rosling *et al.*, 2013).

698 Fungal community composition has been intensively studied in glacier forefields where it was shown
699 that the active fungal community composition changes according to soil developmental stages (Zumsteg *et*
700 *al.*, 2012, 2013b; Rime *et al.*, 2015; Sannino *et al.*, 2020). The diversity of fungi was surprisingly high in
701 barren ground closest to the glacier tongue and was similar to older vegetated soils (Rime *et al.*, 2015;
702 Dresch *et al.*, 2019). Glacier ice is considered as a fungal inoculum source for the earliest ice-related barren
703 ground and for later plant-covered soil (Rime *et al.*, 2016a). Besides the glacier environment, permafrost
704 soils also provide living space for numerous fungi from the prehistoric era (Frey *et al.*, 2016; Luláková *et*
705 *al.*, 2019; Pontes *et al.*, 2020; Frey, 2021). European permafrost soils are dominated by lichenised fungi
706 and basidiomycetous *Rhodotorula*, including the genera *Naganishia*, *Mrakia*, or *Leucosporidium* (Frey *et*
707 *al.*, 2016; Adamczyk *et al.*, 2021; Sannino *et al.*, 2021).

708 Historically, below-ground studies of alpine fungi have focused on ectomycorrhizal (EM) and arbuscular
709 mycorrhizal fungi as well as root associated symbionts of plants. However, there are very few studies on
710 fungal symbionts associated with ericaceous plants, despite the importance of heath vegetation in alpine
711 systems (Kivlin *et al.*, 2017). EM fungi are nevertheless essential for establishment and habitat colonisation
712 by alpine plants such as willows (Nara & Hogetsu, 2004). EM fungi have been examined on a range of
713 hosts, using combinations of linking sporocarps to associated EM tips (*Salix herbacea* L., Graf & Brunner,
714 1996) or selection of EM tips followed by molecular identification (*Dryas* sp. and *Salix* sp. (Kernaghan &
715 Harper, 2001); *Arctostaphylos uva-ursi* (L.) SPRENG. (Krpata *et al.*, 2007); *Bistorta vivipara* (L.)
716 DELARBRE (Thoen *et al.*, 2019)). Gao & Yang (2016) used a cloning approach to examine mycorrhizal
717 fungi on herbaceous plant roots in alpine meadows in Southwestern China. However, metabarcoding
718 studies have provided more comprehensive assessments of root associated fungi on particular host species,
719 including *Arctostaphylos* sp. (Hesling & Taylor, 2013), *Dryas* sp. (Bjorbækmo *et al.*, 2010), *Carex*
720 *myosuroides* VILL. (Mühlmann & Peintner, 2008), *Bistorta vivipara* (Mühlmann, Bacher & Peintner,
721 2008), *Salix* spp. (Ryberg, Andreasen & Björk, 2011). The recent barcoding study by Arraiano-Castilho *et*
722 *al.* (2021) demonstrated that habitat was a stronger determinant than the host plant for EM fungal
723 distribution in alpine habitats. All of these studies highlight the high diversity of fungal symbionts
724 supporting alpine plants.

725 Fungi carry out a multitude of functions in ecosystems, and although they interact with many trophic
726 groups, the major focus has so far been on plant associated symbionts. The importance of fungal/plant
727 interactions in the development of plant communities has been particularly well investigated at glacial
728 fronts in alpine zones using metabarcoding studies in Norway (Blaalid *et al.*, 2012), the Central European
729 Alps (Brunner *et al.*, 2011; Rime *et al.*, 2015), and North America (Jumpponen *et al.*, 2015).

730 Fungal communities in alpine grasslands are primarily affected by edaphic, climatic, and biotic
731 parameters. Specifically, soil pH, soil organic C, N, P, soil water content and electrical conductivity are
732 important soil variables, with snow cover duration also exerting an important influence on fungal richness

(Pellissier *et al.*, 2014; Yang *et al.*, 2017; Malard *et al.*, 2022). The importance of microtopography in alpine zones, particularly differences in snow lie, is widely recognised in structuring plant communities (e.g. Carlson *et al.*, 2015), and a number of studies have also shown topography to be an important driver of soil fungal community composition (Zinger *et al.*, 2009, 2011; Frey *et al.*, 2016). However, this importance is confounded by the close vegetation/fungal relationships. Further studies on individual plant species (see Yao *et al.*, 2013) over a range of topographies may provide greater insights into the direct role of soil conditions on structuring communities.

The strong connections and dependencies between above-ground plant and below-ground fungal communities (see Yao *et al.*, 2013; Tonjer *et al.*, 2021) illustrate that climatic and pollutant-induced changes in alpine plant communities (see Steinbauer *et al.*, 2018) will have major impacts on the associated soil fungi. The upwards migration of treelines (Harsch *et al.*, 2009; Bryn & Potthoff, 2018) and expansion of trees and shrubs into formerly grazed areas (Dibari *et al.*, 2020) will, in particular, have significant impacts on both the taxonomic and functional attributes of alpine soil fungal communities. Similarly, the invasion of alien weed species into alpine vegetation, although currently still limited (Alexander *et al.*, 2016), could lead to alterations of the indigenous fungal communities (Johnston & Pickering, 2001). Lastly, plant richness and diversity are key to fungal alpha and beta diversity in alpine grasslands (Pellissier *et al.*, 2014; Yang *et al.*, 2017; Malard *et al.*, 2022). Similarly, elevated nitrogen deposition induces major shifts in soil fungal functional groups (van der Linde *et al.*, 2018; Zhang, Chen & Ruan, 2018). Coupled with these effects of vegetation change and nutrient availability, there are also direct impacts of changing environmental conditions on fungal communities, with both temperature and moisture being strong drivers of community structure at local (Yao *et al.*, 2013), regional (van der Linde *et al.*, 2018), and global scales (Tedersoo *et al.*, 2014).

(3) Protists

Protists are defined as all eukaryotes that are not plants, metazoans, or fungi (O'Malley, Simpson & Roger, 2013). They form a vast paraphyletic entity spanning the whole eukaryotic tree of life, comprising large, phylogenetically and functionally diverse groups, and are represented mainly by microbial unicellular organisms (Adl *et al.*, 2019; Burki *et al.*, 2020).

Due to their phylogenetic, morphological, and functional diversity, it is difficult to generalise findings on the entire protist community. The total diversity of protists in general is unknown, most species are undescribed, and their distribution and functions are poorly understood. Accordingly, knowledge on soil protists is lagging behind that of many other soil organisms (Geisen *et al.*, 2018; Bonkowski, Dumack & Fiore-Donno, 2019), and this is reflected in the number of studies focusing on protist diversity in alpine soils (Fig. 4, Table S5). Due to the methodological challenges associated with the study of soil microorganisms, many of which cannot be easily grown in the laboratory, the diversity of protists living in

768 oceans and freshwater ecosystems is better documented than that of soil protists. However, high throughput
769 sequencing studies are revealing that their diversity is highest in soils, partly due to the strong heterogeneity
770 of the soil environment and diversity of soil types (Singer *et al.*, 2021). Thus, while numerous studies have
771 explored the diversity of individual protist groups in mountain soils, documentation of this diversity beyond
772 high throughput sequencing approaches still represents a largely open field of research, as is true for minute
773 and microscopic soil organisms in general (Decaëns, 2010). While some protist taxa were described in the
774 European Alps, such as the family Grossglockneriidae (Petz *et al.*, 1986; Foissner, 1999), and *Puytoracia*
775 *jenswendti* SANTIBÁÑEZ ET AL. 2011, a euglyphid testate amoeba discovered on glaciers in the Andes
776 (Santibáñez *et al.*, 2011), the true degree of endemism among alpine protist taxa remains to be determined
777 (Ronikier & Ronikier, 2009).

778 Diversity patterns of soil protists along elevation gradients have primarily been investigated for specific
779 groups, such as testate amoebae, a group of shelled protists commonly used as models for biogeographic
780 studies. Along such gradients, contrasting patterns of distribution were observed: a hump-shaped pattern
781 along the gradient (e.g. Krashevskaya *et al.*, 2007; Krashevskaya, Maraun & Scheu, 2010; Lamentowicz *et al.*,
782 2013), the lowest diversity at mid-elevations (Tsyganov *et al.*, 2022), decreasing richness, diversity, and
783 equitability with increasing elevation (Heger *et al.*, 2016), or no response to elevation (Mitchell, Bragazza
784 & Gerdol, 2004).

785 With the rise of the molecular era, it has become possible to study the response of the whole community,
786 and Shen *et al.* (2014) showed that an elevational gradient induced little shaping force on protistan
787 communities, which were more strongly influenced by edaphic factors such as soil pH. These contradictory
788 patterns reflect the high diversity of protists, but also likely the fact that some groups are poorly recovered,
789 either due to the fact that primers are not totally universal (e.g. Amoebozoa are typically under-estimated)
790 or that the barcode used (e.g. V4 region of the SSUrRNA gene) contains insertions (e.g. some common soil
791 Rhizaria) that make it impossible to use short reads, as in Illumina sequencing (Pawlowski *et al.*, 2012).

792 Protists are paraphyletic and comprise microeukaryotes that are similar in size and shape to yeasts, but
793 also comprise taxa that are several millimetres in size or even reach several decimetres, such as e.g. slime
794 moulds. It is therefore not surprising that protists do not necessarily respond uniformly to environmental
795 gradients. Nonetheless, as in other habitats, the majority of protistan taxa in alpine soils are believed to be
796 small, motile, and cyst forming bacterivores (Oliverio *et al.*, 2020; Kang *et al.*, 2022). Accordingly, only a
797 small effect of elevation on alpha and beta diversities of protistan communities can be expected.
798 Stramenopiles, Alveolates, and Rhizaria (SAR), along with Amoebozoa and Archaeplastida dominate the
799 protist diversity in alpine grasslands (Seppey *et al.*, 2020). In terms of function, consumers are followed by
800 parasites and phototrophs (Mazel *et al.*, 2022). The dominance of consumers in mountain open habitat soils
801 suggests that this functional group could be key in the cycling and turnover of nutrients in this type of
802 ecosystem (Geisen *et al.*, 2015; Oliverio *et al.*, 2020).

803 As it is known from low-elevation soils, edaphic factors (e.g. soil moisture, C content, and soil pH) and
804 the local plant community are strongly determining factors of soil protist communities (Oliverio *et al.*,
805 2020; Aslani *et al.*, 2022). Besides edaphic factors, temperature and slope of mountain systems also drive
806 protist community assemblages (Seppey *et al.*, 2020; Malard *et al.*, 2022). Likewise, Hu *et al.* (2022)
807 showed a strong influence of soil moisture and N content as shaping factors of soil protistan communities
808 at high elevations, while Shen *et al.* (2014) found protist communities to be primarily correlated with soil
809 pH. Only a few studies have aimed at inventorying protist communities in alpine ecosystems (Hu *et al.*,
810 2022; Kang *et al.*, 2022). These studies claim that body size determines the assembly of protist
811 communities, with deterministic factors (e.g. soil acidity, temperature) being more important in protists
812 than in other microbes. Furthermore, Kang *et al.* (2022) showed that the turnover rates among alpine
813 environments were lower in protists than in other microorganisms (bacteria and fungi), which they explain
814 with a higher dispersal rate of motile protists. However, this finding contrasts with floodplains where
815 protists showed higher spatial patterns while bacteria communities changed primarily seasonally (Fournier
816 *et al.*, 2020). Borg Dahl *et al.* (2019) highlighted the importance of plant community as a major determinant
817 of myxomycetes in the European Alps. As such, physicochemical properties and vegetation patterns will
818 differentially shape protists in alpine forests, shrublands, grasslands, pastures, and high alpine zones. To
819 test these suggested trends and hypotheses on protist communities, more targeted inventories are needed
820 across alpine systems. A recent study manipulated precipitation, warming, and nitrogen addition in alpine
821 habitats, revealing that these global change factors fundamentally alter soil protist communities and their
822 abundances. In this study, precipitation and nitrogen input caused an increase in protist diversity and
823 abundance, respectively, while decreased precipitation and warming reduced them (Hu *et al.*, 2022).
824 Further, it can be expected that changes in bacterial, fungal, but also plant and animal communities will
825 cascade to protists (Valencia *et al.*, 2018). Therefore, climate change is expected to alter protist
826 communities in alpine habitats with potential impacts on other components of the soil microbiome and on
827 soil functions (Mazel *et al.*, 2022).

828 The last decades have revolutionised the perspective on soil protist functional roles, which span the
829 whole spectrum from predators, primary producers, parasites, decomposers, phototrophs and saprotrophs
830 (Geisen *et al.*, 2018, 2020). In soils, protists feed on a wide variety of substrates, with heterotrophs
831 representing the most abundant and diverse functional group (Bonkowski *et al.*, 2019). Soil protists were
832 first shown to be key bacterial predators that control bacterial abundances and, via the microbial loop, make
833 nutrients available for plant growth (Clarholm, 1985). However, protist predators occupy different trophic
834 niches by feeding on other microorganisms like bacteria, fungi, algae, micro-metazoa such as nematodes
835 and rotifers (Yeates & Foissner, 1995; Gilbert *et al.*, 2000; Jassej *et al.*, 2013; Geisen *et al.*, 2015;
836 Estermann *et al.*, 2023), and other protists (Seppey *et al.*, 2017; Geisen *et al.*, 2018; Bonkowski *et al.*,

837 2019). Hereby, phagocytosis appears to be the main mechanism for nutrient acquisition (Singer *et al.*,
838 2021).

839 Bacterivorous taxa may dominate the protist community in many cases (Oliverio *et al.*, 2020; Aslani *et*
840 *al.*, 2022), but the dominant feeding habits can be expected to match the available resources and especially
841 the bacteria to fungi ratio, which responds to soil pH (Rousk, Brookes & Bååth, 2009). Hence, fungivores
842 are likely more common in subalpine (e.g. conifer-dominated forests) and lower alpine (e.g. ericoid heath)
843 habitats, as perfectly illustrated by the obligate fungivorous grossglocknerid ciliates that were discovered
844 in the European Alps (Petz *et al.*, 1986; Foissner, 1999).

845 Soil protists, including crop pathogens like *Phytophthora infestans* (MONT.) DE BARY, have a broader
846 role as parasites, potentially affecting plant or soil animals. However, the diversity and interactions of these
847 protist parasites remain understudied. Apicomplexa parasites of invertebrates and vertebrates, strongly
848 dominate soil protist diversity in tropical forests and this dominance is thought to reflect the overall
849 invertebrate diversity throughout the ecosystem, from soil to canopy (Mahé *et al.*, 2017). In line with this,
850 a study in the Swiss Alps showed that the diversity of Apicomplexa in various alpine habitats correlated
851 positively with the diversity of their putative metazoan hosts (Singer *et al.*, 2020). The relative contribution
852 of parasites to the total protist community compared to other functional groups was, however, shown to
853 decrease with increasing elevation, likely due to the reduction in host density with elevation (Mazel *et al.*,
854 2022).

855 Phototrophic protists, like *Chlorella* and *Trebouxia*, are common as symbionts in lichens, but also as
856 free-living forms at the soil surface (Jassey *et al.*, 2022). However, the abundance of free-living
857 phototrophic protists (and their predators) is highest in moist (e.g. peatlands) and open (e.g. arid or alpine)
858 vegetation (Gilbert *et al.*, 1998; Seppey *et al.*, 2017). In arid habitats, including patchy alpine vegetation,
859 phototrophic protists contribute to the formation of biocrusts, which are major contributors to organic C
860 and N fixation (Dickson, 2000) and reduce soil erosion (Evans & Johansen, 1999). While soil protists have
861 long been neglected in soil microbiological studies (Geisen *et al.*, 2020), they now are the focus of an
862 increasing number of studies as their importance as determinants of plant performance is established
863 (Bonkowski, 2004; Gao *et al.*, 2019). Thus, protists are now recognised as important elements in soils
864 ecosystems due to their role in the microbial food web and nutrient cycling (Adl & Gupta, 2006; Geisen *et*
865 *al.*, 2016) and their contribution to biogeochemical cycles, especially C (Geisen *et al.*, 2020) and silica
866 (Aoki, Hoshino & Matsubara, 2007).

867

VI. SOIL INVERTEBRATES

KEY ASPECTS

- The treeline ecotone harbours a high diversity of soil macro-, meso-, and micro-invertebrates, as species from both forest and grassland ecosystems coexist. At higher elevation, the shallow soils are mainly inhabited by soil meso- and micro-invertebrates.
- Faunal diversity generally decreases with increasing elevation, as climatic and energetic conditions become more challenging. Some taxa reach their upper distribution limits (e.g. earthworms and millipedes in the high alpine zone).
- Essential ecosystem functions are carried out by only a few key taxa (e.g. litter decomposition in the high alpine is mainly carried out by Nematocera larvae and soil meso-invertebrates).
- Soil food webs in high alpine soils are simple, with fewer interactions compared to lowland soils. Omnivorous and opportunistic feeding habits have increased to ensure energy intake.
- Extensive grazing by livestock and wild ungulates can improve conditions for soil fauna by providing nutritious manure and reducing cover of recalcitrant dwarf shrubs.
- We found 205 publications dealing primarily with alpine soil fauna (i.e. 118 for macro-, 52 for meso-, and 35 for micro-invertebrates), mainly from the mountain regions of Central & Southern Europe (42.9%), Central Asia (15.6%), and Australia & New Zealand (13.2%); see Fig. 5 and Table S6.

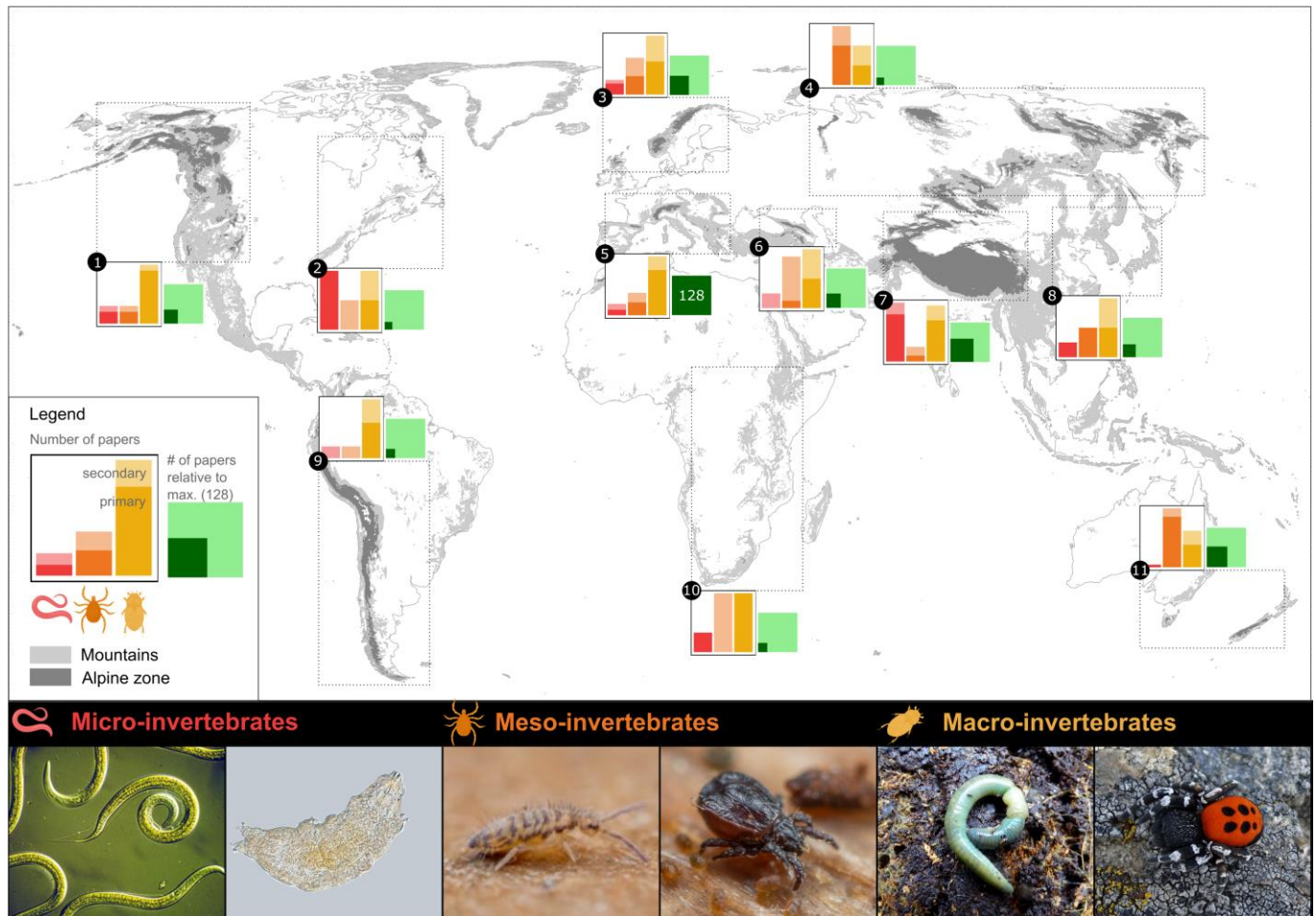


Fig. 5. Global map of scientific articles focusing on invertebrates in alpine mountain soils. Number of publications are given per invertebrate group and relative to the maximum of papers found (Central & Southern Europe): the dark-coloured part of the bar represents those papers where the organismic group was likely the primary object, the light-coloured part represents those papers where the organismic group was mentioned, but not as the main subject of the publication. See Appendix S1 for a detailed description of the methods and full list of publication numbers per region and soil organism group. Photos from left to right: Micro-invertebrates: images of Nematoda (credit: CSIRO Entomology), and a Tardigrada *Macrobiotus* sp. (credit: Michala Tůmová) through microscopes; Meso-invertebrates: the Collembola *Entomobrya nivalis* and the Acari *Platynothrus pelifer* (credit: both Frank Ashwood); Macro-invertebrates: the ‘green’ earthworm *Aporecctodea smaragdina* inhabits calcareous mountain soils in the European Alps and Dinaric Alps, male velvet spider *Eresus sandaliatus* found in alpine dry pastures in the Central European Alps (credit: both Michael Steinwandter).

885 In general, soil invertebrates belong to a wide range of taxa. Their diversity is particularly high close to
 886 the treeline, as representatives of all size classes (micro-, meso-, and macro-invertebrates, (Orgiazzi *et al.*,
 887 2016) are found and grassland species co-occur with forest species, especially in intertwined dwarf shrub

888 habitats. Macro-invertebrates (taxa with a mean body size > 2 mm, mainly earthworms, spiders, myriapods,
889 isopods, ants, and insect larvae) decrease in numbers with increasing elevation due to climatic and
890 topographic factors. Vegetation cover and the amount of soil decrease, particularly limiting soil macro-
891 invertebrates that require a vegetation cover that produces litter material and/or the physical habitat space
892 that is provided by mature soils. Meso- (mainly collembolans, mites, and enchytraeids) and micro-
893 invertebrates (mainly nematodes, rotifers, and tardigrades) can still be abundant in shallow high-elevation
894 soils even though habitat space and litter inputs from vegetation are reduced.

895 Compared to soil microbiota, data on soil fauna are scarce and often limited to ground-dwelling taxa
896 (Burton *et al.*, 2022). Soil fauna studies focusing on alpine and high-elevation habitats are especially rare.
897 Available data pertain primarily to alpine regions in Central & Southern Europe (i.e. 42.9%, Fig. 4 and
898 Table S6) such as the Central European Alps (e.g. Puntischer, 1980; Meyer & Thaler, 1995; Koch &
899 Erschbamer, 2010; Gobbi *et al.*, 2020; Seeber *et al.*, 2021), Central Asia (15.6%) such as the Tibetan
900 Plateau (e.g. Wu, Zhang & Wang, 2015; Devetter *et al.*, 2017), and Australia and New Zealand (13.2%,
901 e.g. Salmon, 1940; Hammer, Foged & Nørvang, 1966; Houston & Greenslade, 1994; Minor *et al.*, 2016;
902 Mesibov, 2018; Green & Slatyer, 2020), while alpine regions in the Americas (i.e. Rocky Mountains,
903 Appalachians, and Andes), Africa (i.e. Drakensberg), and the Caucasus remain understudied (but see
904 Armstrong & Brand, 2012; Kokhia & Golovatch, 2020). We were able to find only five soil fauna
905 publications for each of these alpine regions (Table S6, Appendix S1). A similar outcome was found for
906 the alpine region of Siberia (i.e. North Asia), where information is locally available but mainly published
907 in Russian and therefore not indexed in the ‘Web of Science’ portal.

908 In alpine environments, large soil fauna is generally sampled by installing pitfall traps (macro-, partially
909 also meso-invertebrates), by taking soil core samples (all groups), by suction sampling (ground-dwelling
910 meso-invertebrates), as well as via hand sorting and hand sampling (macro-invertebrates); pitfall traps are
911 preferably used in higher elevations as soil is getting scarce and shallow. To cope with methodological and
912 logistical limitations, additional approaches such as soil biodiversity indices (e.g. QBS-ar, Maienza *et al.*,
913 2022) and DNA metabarcoding (e.g. via environmental DNA (eDNA), Rota *et al.*, 2020) are increasingly
914 applied also in alpine habitats. Amongst the alpine soil fauna species described to date, some are rarely
915 found and observations are often based on occasional records. Such observations can even lead to new
916 discoveries for alpine regions due to the scarcity of research such as the carabid beetle *Orthoglymma*
917 *wangapeka* LIEBHERR, MARRIS, EMBERSON & SYRETT & ROIG-JUÑENT, 2011 (Liebherr *et al.*, 2011) and the
918 oribatid mite *Crotonia ramsayi* COLLOFF, 2015 (Colloff, 2015) for New Zealand, the isotomid springtail
919 *Skadisotoma inpericulosa* GREENSLADE & FJELLBERG, 2015 (Greenslade & Fjellberg, 2015) for Australia,
920 and *Opetiopalpus sabulosus* MOTSCHULSKY, 1840 (Steinwandter *et al.*, 2019). A high percentage are
921 regionally endemic or found in restricted geographical areas, as observed in the European Alps (e.g.
922 Komposch, 2011), in Australasia (Boyer & Giribet, 2009), and in the Drakensberg of Southern Africa

(Armstrong & Brand, 2012). These species are mainly relicts of the last glaciations that survived in nunataks and other refugia offered by highly heterogeneous mountain topography (Brighenti *et al.*, 2021); in subsequent interglacial periods, these alpine invertebrates have expanded extensively (Hill *et al.*, 2009). For Australasian alpine taxa, a deeper phylogeographic structuring was shown compared to European and North American ones, possibly reflecting less intense glaciation and a higher availability of refuges during glaciation events (King *et al.*, 2020). Colonisation processes in high alpine areas can be surmised by observing the colonisation of alpine land when glaciers retract (Koch & Kaufmann, 2010; Hågvar *et al.*, 2020). The first to re-colonise the bare land, which is comparable to quarries, are mostly agile ground-dwelling predators (e.g. carabid beetles, harvestmen, lycosid spiders) depending presumably on windblown animals as food sources, followed by the meso-invertebrates (springtails and oribatid mites) after 30 years. Finally, larger detritivores (millipedes and Nematocera larvae) appear when the soil and the vegetation are more developed (Kaufmann, Fuchs & Gosterxeier, 2002).

(1) Macro-invertebrates

The diversity of soil macro-invertebrates – often referred to simply as soil macrofauna – is generally lower in high alpine grasslands than in the alpine and subalpine zone and often peaks in ecotone areas (i.e. the transition zones at the treelines and open alpine grasslands; Fontana *et al.*, 2020; Steinwandter & Seeber, 2023). Elevation and vegetation are the primary determinants of alpine soil macro-invertebrate communities (Kooch & Noghre, 2020; Steinwandter *et al.*, 2022; Xie *et al.*, 2022; Lavelle *et al.*, 2022). Earthworms (Lumbricidae), for instance, show a hump-shaped distribution peaking at the treeline ecotone area (Fontana *et al.*, 2020; Gabriac *et al.*, 2023). Earthworm abundance decreases in alpine grasslands (Seeber *et al.*, 2005; Steinwandter *et al.*, 2018), likely because of their limited tolerance to the cold temperatures encountered at higher elevations (Meshcheryakova & Berman, 2014). Additional influencing factors include vegetation attributes such as plant life-forms and host-plant distributions (e.g. Edwards & Arancon, 2022), as well as soil attributes such as pH, clay, and water content. Also, poorly developed soils provide limited habitat space for burrowing species. Yet, abundances and species diversity may increase with the presence of grazing livestock and wild mammals, whose dung represents a readily available food source for all decomposer taxa (Bueno & Jiménez, 2014; Steinwandter *et al.*, 2018; Jászayová *et al.*, 2023).

Millipedes (Diplopoda) are litter-dwellers and therefore mostly found in dwarf shrub-rich grasslands and ecotones above the treeline, where they find the mature and stable soils they prefer as well as more abundant food resources such as litter and organic debris (Onipchenko & Zhakova, 1997; Steinwandter *et al.*, 2018; Gobbi *et al.*, 2020; Kokhia & Golovatch, 2020). Most millipede species reach their upper limit of distribution at the transition between the subalpine and alpine zones and are rare or even completely absent in high alpine habitats. Soil core samples from high elevations generally contain few to no millipede

958 specimens, making estimates of their densities difficult. However, millipedes (and soil invertebrates in
959 general) are easier and more efficiently detected in high alpine environments by using pitfall traps or hand
960 sampling and are therefore occasionally found at higher elevations (e.g. *Beronodesmoides* spp.
961 (Polydesmida: Paradoxosomatidae) up to 4500 m in Nepal (Golovatch, 2015). Millipede species inhabiting
962 high elevations mainly belong to the orders Polydesmida, Chordeumatida, and Julidae (Beron, 2008, 2016).
963 In the Central European Alps, species found in higher elevations belong mainly to Chordeumatida, which
964 are described to be petrophilic with a preference for cold mountain areas and which are active beneath the
965 snow (Meyer, 1980). These millipedes were found in high numbers at sites up to 3000 m (Steinwandter &
966 Seeber, 2023), while other myriapods such as centipedes (Chilopoda) were almost absent. Other millipede
967 species that frequently inhabit European mountain soils and can be found at high elevation include eurytope
968 millipede species such as *Ommatoiulus sabulosus* (LINNAEUS, 1758) (Julida: Julidae) as well as specialists
969 such as the endemic *Glomeris transalpina* KOCH C. L., 1836 (Glomerida: Glomeridae); both are known to
970 inhabit alpine rocky sites and soils even up to 3000 m. However, elevational limits may now change with
971 ongoing global warming: Gilgado *et al.* (2021) recently described ten millipede species whose elevational
972 limits in the Swiss Alps have expanded upwards by several 100 metres over the last century.

973 Surface-active and highly mobile and agile predators, such as spiders, harvestmen, and some beetle
974 families are abundant representatives of the high alpine soil fauna (Kaufmann *et al.*, 2002; Hågvar *et al.*,
975 2020; Gilgado *et al.*, 2022) and seem not to depend on mature soils but rather on available prey. Numerous
976 studies have investigated the diversity of beetles in mountain soils, but the majority focus on a few widely
977 distributed and well-known families (e.g. Carabidae, Staphylinidae, and Scarabaeidae). The density,
978 diversity, and distribution of predatory beetles are affected by a wide range of factors such as biotic
979 interactions, vegetation (Negro *et al.*, 2010; Yu *et al.*, 2013), abiotic factors such as temperature and
980 moisture (Yu *et al.*, 2013), historical factors such as climatic variability and topographical changes, and
981 human activities (Larsen, 2012; Brandmayr & Pizzolotto, 2016). Further, topographic isolation may boost
982 beetle diversity as it was found by Armstrong & Brand (2012) on isolated peaks (i.e. > 3000 m) of the
983 Drakensberg (Afro-alpine Region), where leaf- (Chrysomelidae), ground- (Carabidae), and sap beetles
984 (Nitidulidae) dominated.

985 In the case of ants (Hymenoptera: Formicidae), as with other soil fauna, their presence and abundance
986 decrease with increasing elevation in alpine settings, where severe filtering can be detected both on
987 taxonomic as well as functional and phylogenetic diversity (Glaser, 2006; Machac *et al.*, 2011; Chaladze,
988 2012; Reymond *et al.*, 2013; Bishop *et al.*, 2014). Elevational limits to occurrence are related to the ability
989 of ants to cope with low temperatures (Bishop *et al.*, 2017). However, while ant colonies tend to occur in
990 the lower alpine area and become increasingly absent in high alpine areas, some individuals (mainly
991 specimens from the winged 'alates' caste) may be transported upwards by wind. Overall, ant diversity peaks
992 at mid-elevation and decreases constantly – and often linearly – with increasing elevation (Subedi & Budha,

993 2020). Similar results were found for the Maloti-Drakensberg in Southern Africa by Bishop *et al.*, (2014)
994 who attributed the spatial and temporal differences primarily to temperature. In the European Alps, most
995 ant species occurring in the alpine habitat are also present in the higher montane forest belt (Glaser, 2006),
996 and a higher species diversity was recorded in the treeline ecotone (Guariento & Fiedler, 2021).
997 Interestingly, a high number of social parasitic ant species are reported from alpine habitats without a clear
998 explanation so far, except that the harsher environment might positively select for such life history traits
999 (Dunn *et al.*, 2009; Schifani *et al.*, 2021). In alpine grasslands, the effect of ants on soils is mostly related
1000 to nest construction, since most taxa build their nests in the soil, causing soil turnover as well as nutrient
1001 accumulation and influencing the vegetation (Wang *et al.*, 2017; Zhao *et al.*, 2020). Ants strategically
1002 establish their nests beneath rocks, leveraging the warmth absorption and insulation (McCaffrey & Galen,
1003 2011). Therefore, the rock features (e.g. distribution, shape) represent an important factor for the
1004 establishment of ant nests. Studies investigating the functional role of ants indicate higher trophic levels in
1005 the alpine environment (Spotti *et al.*, 2015; Guariento, Martini & Fiedler, 2018), even suggesting
1006 intraspecific dietary shifts (Guariento, Wanek & Fiedler, 2021).

1007 Other insect taxa such as larvae of lower flies (Nematocera) increase in numbers at higher elevations.
1008 They can – at least in parts – carry out crucial ecological functions such as litter decomposition and
1009 bioturbation which are usually provided by detritivores such as millipedes and earthworms (Meyer &
1010 Thaler, 1995; Kitz *et al.*, 2015).

1012 (2) Meso-invertebrates

1013 Soil meso-invertebrate communities – often referred to simply as soil mesofauna – are mainly composed
1014 of springtails (Collembola), mites (Acari), other small arthropods, and potworms (Enchytraeidae) (Potapov
1015 *et al.*, 2022). Of these, springtails are the most widespread and abundant invertebrates, occurring in almost
1016 all terrestrial ecosystems (Hopkin, 1997; Deharveng, 2004). They play essential roles in many soil
1017 ecosystem processes, such as C and N cycling, soil microstructure formation, and plant litter decomposition.
1018 Collembola density and diversity vary significantly with environmental factors and plant community
1019 composition, and in the shallow alpine soils they inhabit mostly the litter and upper soil layers (Seeber *et*
1020 *al.*, 2021; Xie *et al.*, 2022).

1021 In general, the composition and abundance of meso-invertebrate communities in soil are dependent on
1022 elevation (Striganova & Rybalov, 2008; Jiang, Yin & Wang, 2015; Khabir *et al.*, 2015; Schatz, 2017;
1023 Winkler *et al.*, 2018), soil properties (van der Merwe *et al.*, 2020), the identity of plant species and the
1024 variability of vegetation communities (Eo *et al.*, 2016; Xie *et al.*, 2022), all of which can lead to a high
1025 spatial heterogeneity with many local microhabitats. Furthermore, factors related to climate change, such
1026 as temperature (Harte, Rawa & Price, 1996; Alatalo *et al.*, 2017) and reduced soil water availability
1027 (Sylvain *et al.*, 2014), as well as (anthropogenic) disturbances may also affect soil mesofauna diversity and

1028 communities. Habitat management (Kooch, Shah Piri & Dianati Tilaki, 2021), tourist activity (Meyer,
1029 1993; Kopeszki & Trockner, 1994), cattle trampling and grazing (Hauck *et al.*, 2014; Risch *et al.*, 2015),
1030 fire (Driessen & Kirkpatrick, 2017), soil erosion (Meyer, 1993; van der Merwe *et al.*, 2020), and pollution
1031 (Rusek, 1993; Visioli *et al.*, 2019) all affect the meso-invertebrates living in alpine grasslands, suggesting
1032 that environmental filtering is the predominant process shaping soil meso-invertebrate communities (Visioli
1033 *et al.*, 2019).

1034 In the nival zone, the soil fauna community is composed almost exclusively of meso-invertebrates –
1035 springtails, mites, and by region additionally by predatory false scorpions (Pseudoscorpiones), e.g. in
1036 European Alps, Carpathian Mountains. Mesofauna distribution is scattered and limited to favourable
1037 refugia such as congregations of detritus or cushion plants (Meyer & Thaler, 1995). Some specialist taxa
1038 are adapted to snowbeds, which can persist for most of the year (Seeber *et al.*, 2021). These species rely on
1039 aeolian food sources (i.e. wind-blown debris) or prey on small animals searching for this food; the different
1040 taxa are active at different times of the day as extreme environmental conditions restrict their activity
1041 (Mann, Edwards & Gara, 1980).

1042 1043 **(3) Micro-invertebrates**

1044 Soil micro-invertebrates (taxa < 0.1 mm in size) – simply referred to as soil microfauna – mainly
1045 comprise roundworms (Nematoda), rotifers (Rotifera), and water bears (Tardigrada). Little research on
1046 these tiny soil invertebrates has been conducted in alpine regions (Devetter *et al.*, 2017), however, a global
1047 distribution map of nematodes revealed a positive relationship between organic C content in mountain soils
1048 and abundance of nematodes (van den Hoogen *et al.*, 2019). Micro-invertebrates are generally favoured in
1049 fertile soils with high contents of N, P, and organic matter (Devetter *et al.*, 2017), and are easily affected
1050 by disturbances such as soil degradation and shrub encroachment after abandonment (Hu *et al.*, 2017; Wu
1051 *et al.*, 2017; Wang *et al.*, 2018)(Hu *et al.*, 2017; Wu *et al.*, 2017; Wang *et al.*, 2018). Recently, Poraziska
1052 *et al.* (2021) showed that soil nematodes expand their distribution ranges with elevation by following
1053 expanding plant species, and as plant communities become more complex and diverse even at higher
1054 elevations, a more diverse nematode community may increasingly contribute to C and N sequestration.
1055 Further, Li *et al.* (2023) found that soil nematodes – which are generally water-bound – respond positively
1056 to higher precipitation and soil water content in alpine grasslands of the Tibetan Plateau, with higher
1057 trophic-level nematodes (i.e. omnivores, carnivores) showing stronger effects than lower trophic-level
1058 nematodes (i.e. bacterivores, fungivores).

1059 1060 **(4) Adaptation strategies of fauna to mountain soils**

1061 The conditions in high alpine areas can be hostile to animal life, but soil taxa have adapted over a long
1062 time and have developed strategies to cope with the harsh and varying climate. Many taxa have black, dark

1063 brown, or dark grey body colour (e.g. beetles, spiders) (Armstrong & Brand, 2012), an adaptation that
1064 allows larger cold-blooded mountain animals to better absorb sunlight and therefore energy. Appendages
1065 and legs are often shorter than those of the same species and groups living in lower habitats. Wing size is
1066 also often reduced (i.e. a higher degree of brachyptery or winglessness), for example in carabid
1067 communities of high alpine habitats (Pizzolotto, 2016). Due to the long duration of snow cover, alpine soil
1068 invertebrates show increased cold resistance, behavioural thermoregulation, and actively seek thermally-
1069 buffered microhabitats (Dillon *et al.*, 2006; Schoville *et al.*, 2015; Buckley *et al.*, 2015). Yet, individuals
1070 often search for food on the snow surface or in more favourable locations that can only be reached by
1071 crossing snowfields, thus, the risk of hypothermia is often high.

1072 Beside physiological adaptations, high alpine soil fauna typically show more generalist diets (i.e.
1073 omnivory) due to the low availability of food resources. Predation seems to be driven by the presence and
1074 abundance of a given prey. For example, in extremely high-elevation environments such as glacier
1075 forefields, carabid beetles of *Nebria* spp. and lycosid spiders of *Pardosa* spp. prey on springtails (König,
1076 Kaufmann & Scheu, 2011; Sint *et al.*, 2019; Hågvar *et al.*, 2020), which are specifically tied to the
1077 geomorphology of these habitats (i.e. rough stones that can trap food and prevent flushing, Buda *et al.*,
1078 2020). Food limitation in such environments results in simpler and more reduced food webs compared to
1079 lowland habitats (König *et al.*, 2011; Raso *et al.*, 2014; Steinwandter *et al.*, 2018). Species which are
1080 usually saprotrophic also include animal food sources (e.g. exuvia, carcasses, tissue parts) in their diet and
1081 may feed on living animal tissue as plant-based litter is rare or even absent. For predators such as carabid
1082 beetles living in barren high alpine soils with limited number of prey (i.e. mainly springtails), increased
1083 intraguild and intraspecific predation has been observed to sustain nutritional needs (Raso *et al.*, 2014).
1084 Additional food can also come from airborne sources, including flying and wind-carried insects, as well as
1085 detritus (Růžička & Zacharda, 1994; Hågvar *et al.*, 2020). However, specialised predation to efficiently
1086 intercept the most abundant prey has also evolved, as in the case of the carabid genera *Leistus* and
1087 *Notiophilus*, which trap springtails with their antennae setae (i.e. setal traps, Bauer, 1985). Additional
1088 adaptations pertain to the invertebrates' life history. For example, the life cycle of millipedes and other soil
1089 invertebrates can be interrupted and postponed to spring of the following year if it cannot be completed
1090 within a single season (Meyer, 1985; Sømme & Block, 1991; Valle *et al.*, 2020). Also, parthenogenesis is
1091 widespread, especially among the soil meso-invertebrates (e.g. springtails and mites), allowing them to
1092 thrive when the conditions are more variable (Pan *et al.*, 2023).

VII. KNOWLEDGE GAPS AND RESEARCH OPPORTUNITIES

A number of recent papers discuss data, knowledge, and policy gaps in soil biodiversity science at a global scale (Guerra *et al.*, 2020, 2021, 2022), but there has been no such contribution for alpine soils so far. This is the case despite the critical importance of healthy mountain soils for human safety and wellbeing and for the global provisioning of essential goods and services such as clean water. In this section, we address this gap and identify three main fields/topics for future soil biodiversity research and policymaking in mountains. We put a special emphasis on mountain characteristics that are key but also challenging for soil biodiversity research in mountains (see Klein *et al.*, 2019). These include the typical elevational gradients encountered in mountains, their remoteness and simultaneous exposure to global change, and their global distribution.

(1) Opportunity 1: Increase and improve mountain soil biodiversity data

Premise: In line with recent global analyses, our synthesis indicates that data on mountain soil biodiversity is generally sparse and biased (Figs. 1 and 3–5) towards specific geographic regions (Central Asia and Central Europe) and taxonomic groups (mostly soil microbiota). In particular, it points to limited data for groups such as soil invertebrates that are more exhaustively described in other biomes (Geisen *et al.*, 2017, 2018; Eisenhauer *et al.*, 2022). This lack of data on species diversity and occurrence in mountain soils constitutes an important gap in our knowledge of biodiversity on Earth. It causes species to be overlooked by science, conservation, policy, and advocacy, even if they are possibly on the verge of extinction and/or play critical roles in supporting ecosystem functions. This is particularly important in soils, where interactions among taxa are ubiquitous and essential for species persistence and ecological functions (e.g. Bardgett & van der Putten, 2014). As soil organisms and keystone species disappear, the functioning of entire ecosystems could be disrupted, threatening humanity at large (Jousset *et al.*, 2017; Banerjee, Schlaeppli & van der Heijden, 2018; Chen *et al.*, 2020; Guerra *et al.*, 2021).

The observed lack of species data also comes with the risk of overlooking invasive species that could alter soil properties and represent a threat to native species (e.g. the earthworm *Amyntas agrestis* (GOTO & HATAI, 1899) in the Great Smoky Mountains (Appalachian Mountains, Snyder, Callahan & Hendrix, 2011)). In addition to the absence of information on the mere existence of many species, limited (long-term) data on trends in populations, species distributions, and community composition further jeopardise the ability of science and policy to detect, interpret, and ultimately address or prevent effects of global change on mountain soils and ecosystem functions. It equally hinders the detection of potentially unexpected effects of nature conservation. Whereas species distribution and range expansions are increasingly better documented in particular for plants (e.g. Rumpf *et al.*, 2018; Staude *et al.*, 2022), such information hardly exists for soil biota, and temporal variation in diversity along elevational, topographical or other ecological gradients is largely unknown (e.g. see Seppey *et al.*, 2020 for soil protists). Furthermore,

1130 limitations in spatial representativeness and coverage of taxonomic groups in soil biodiversity data
1131 constrain our capacity to understand mountain soil systems and their response to change based on
1132 comparative analyses at multiple biogeographic scales. Given the worldwide occurrence of mountains, the
1133 differences between mountain ranges, and the existence of differences even between the south- and north-
1134 facing slopes of individual mountains, such comparative approaches are both important and particularly
1135 interesting. Importantly, these gaps in knowledge also hamper the establishment, design, and prioritisation
1136 of monitoring efforts as well as the integration of soil biodiversity in “Red Lists”.

1137 Directions: We support previous calls for a better geographic and taxonomic coverage in soil biodiversity
1138 research and for prioritising long-term monitoring of life in mountain soils at national (Guerra *et al.*, 2020,
1139 2021; Eisenhauer *et al.*, 2022) and global (Maestre & Eisenhauer, 2019) scales. Multiple options exist for
1140 increasing and improving mountain soil biodiversity data (see also Hochkirch *et al.*, 2021). One resides in
1141 molecular approaches such as DNA or RNA barcoding and the use of metagenomics and
1142 metatranscriptomics. These methods offer great opportunities, in particular for the detection and
1143 identification of microbiota as well as for attributing them to threat categories (e.g. Guerra *et al.*, 2021).
1144 While in use for bacteria and fungi already (see Section V), they could also deliver much needed
1145 information for other soil organisms in mountains. Another option to increase species discovery rates
1146 resides in the identification of mountain locations where unknown taxa are most likely to be encountered
1147 (e.g. Delgado-Baquerizo, 2019; Verdon *et al.*, 2023). Such an effort is particularly interesting in remote
1148 locations, where *in situ* sampling is particularly challenging. Similar approaches for the identification of
1149 sampling locations based on the intersection of spatial datasets of mountain extents (Snethlage *et al.*, 2022),
1150 key environmental variables, and abiotic factors (e.g. soil temperature and type) might also serve the
1151 prioritisation of appropriate sites for long-term monitoring of mountain soil species and communities along
1152 elevational gradients. Furthermore, as suggested by van der Putten *et al.* (2023), an alternative to identifying
1153 species is to qualify soil biota based on traits and thereby more readily understand what ecosystem functions
1154 are likely to be lost as species go extinct. A trait-based approach could be particularly interesting in
1155 mountains where harsh environmental conditions, including extreme temperature (gradients) and
1156 biophysical stressors such as recurrent avalanches, are likely determining unique sets of traits.

1157
1158 **(2) Opportunity 2: Increase and improve information on the environmental determinants of**
1159 **biodiversity in mountain soils, the drivers of change in mountain soil biodiversity, and the**
1160 **consequences of these changes**

1161 Premise: The occurrence and diversity of life forms in mountain soils are strongly determined by
1162 environmental factors, including temperature, snow cover, precipitation, humidity and wind, as well as
1163 factors such as soil properties (e.g. pH, organic matter quantity and quality, parental material composition).
1164 Accordingly, as these factors are changing in response to changes in climate, land-use, and other drivers

1165 such as pollution, soil communities are expected to experience novel life conditions influencing their
1166 distribution, dynamics, survival potential, and functions (e.g. Feng *et al.*, 2023). In that context, glacial
1167 forefields represent newly forming ecosystems of particular interest and need of protection (Bosson *et al.*,
1168 2023; Tollefson, 2023). Additionally, (expected) change in the elevation range limits, distribution, and
1169 community composition of vascular plants in response to global change are likely to have additional
1170 consequences on soil organisms, whose ecology and life histories are tightly associated with plants.
1171 Furthermore, as environmental factors such as temperature and soil moisture determine not only the
1172 occurrence and diversity of organisms but also specific biochemical cycles such as the production of
1173 methane (e.g. Hofmann, Reitschuler & Illmer, 2013), feedback loops are likely to magnify effects of
1174 climate and land-use change and thereby exacerbate the exposure of soil biota to unprecedented and extreme
1175 environments. Such feedback loops or cascading effects are further exacerbated by the reciprocal effects of
1176 organisms on their environment (e.g. pedogenic effects of cryptogams, Musielok *et al.*, 2021).

1177 Directions: Identifying the impacts of global change and anthropogenic activities on mountain soil
1178 biodiversity is essential to safeguard soil functions, services, and health (Arora, 2023). In that context,
1179 considerable improvements are needed in the spatial resolution, temporal coverage, and accuracy of
1180 information on fundamental variables such as soil type, temperature, moisture, pH, and precipitation in
1181 mountains (e.g. Randin *et al.*, 2020). We also join others (e.g. Bouaicha *et al.*, 2022; Eisenhauer *et al.*,
1182 2022) in calling for improved data and remote-sensing products on less common drivers of soil biodiversity,
1183 such as pollution by microplastics, chemicals, and heavy metals. Such data are particularly important in
1184 mountain regions, where global atmospheric transport of micropollutants as well as human activities, such
1185 as mining, pastoralism, and tourism are major sources of pollution (Schmeller *et al.*, 2022), impacting soils
1186 and their biodiversity. Improved data are further important to identify and better understand the interactions
1187 of global change drivers, both in space but also in time, as exposure to anthropogenic factors typically
1188 varies over the seasons (e.g. pastoralism in the summer and ski runs in the winter). Moreover, given the
1189 high level of interactions between soil organisms, which causes conditional dependencies between groups
1190 of soil biota and the environment, a holistic approach is needed when making inferences about possible
1191 drivers of change or responses to given environmental variables. Accordingly, understanding the response
1192 of soil biota to global change calls for the joint monitoring and analysis of multiple groups and species in
1193 their interaction with each other and their environment (Eisenhauer *et al.*, 2022). Given the worldwide
1194 distribution of mountains (Körner *et al.*, 2017; Snethlage *et al.*, 2022), we further recommend a
1195 comparative approach to global change research in mountain soils and take advantage of the fact that
1196 mountains across the world differ in their environmental conditions, their history of exposure to human
1197 pressure, as well as in their environmental gradients. For example, whereas extreme temperatures are not
1198 yet recurrent in most mountain regions worldwide, exposure to high temperatures and extreme dryness is
1199 typical in certain ranges such as in the Mediterranean or inner European Alps, where soils and their biota

1200 show specific community composition and species adaptations in response to these conditions (Praeg *et al.*,
1201 2020). Accordingly, comparative analyses of soil biodiversity, as well as of genetic and trait diversity across
1202 mountain ranges are likely to yield interesting understanding with respect to evolutionary potential of
1203 terrestrial ecosystem (Bardgett & van der Putten, 2014) in the face of global change. Similarly, beyond the
1204 assessment of niche variation along environmental gradients within mountains (e.g. Malard *et al.*, 2022),
1205 the quantification and comparison of niche properties across environmental gradients in different mountain
1206 ranges is expected to help evaluate the potential influence of global change on taxa and communities as
1207 well as improving our capacity to predict the fate of ecosystems and thereby inform conservation (e.g. Mod
1208 *et al.*, 2021). Biogeographic studies and palaeoecological analyses might further provide useful information
1209 on the distribution of species over evolutionary times and on the resilience of mountain soils to changes in
1210 climate.

1211 1212 **(3) Opportunity 3: Increase policy-relevant mountain soil biodiversity science and improve mountain** 1213 **soil conservation and policies**

1214 Premise: Belowground biodiversity is essential to healthy soils, which in turn are crucial for food
1215 production, aboveground biodiversity, climate control, and human health and security (Banerjee & van der
1216 Heijden, 2023). Due to the intrinsic connection between terrestrial and aquatic environments, soil
1217 biodiversity and healthy soils are particularly important in mountains in their role as water towers. However,
1218 despite their importance and the growing interacting impacts of climate and land-use change, pollution, and
1219 overexploitation (e.g. mining) in mountain regions, mountain soils and their biodiversity – even more so
1220 than lowland soils – remain only poorly addressed in laws, restoration, and conservation policies (but see
1221 Stanchi *et al.*, 2023). One of the numerous challenges associated with soil conservation and protection and
1222 with formulating laws and guidelines for sustainable use of mountain soils is that soils are connected across
1223 national borders and continents by human activity (van der Putten *et al.*, 2023), calling for international
1224 agreements. An additional difficulty specific to mountains is their transboundary nature, with many
1225 mountain ranges crossing national borders, which further requires reinforced international collaboration in
1226 the establishment of meaningful policies. In that context, the Soil Conservation Protocol and the Soil
1227 Working Group of the Alpine Convention represent valuable efforts. The difficulty of collecting data in
1228 mountains further contributes to making their soils and the diversity of species they host a blind spot in
1229 science, conservation, and policymaking. The observation that most parties to the Convention for Biological
1230 Diversity (CBD) have no national target explicit to soil conservation and biodiversity (Guerra *et al.*, 2021)
1231 and that the protection and conservation of soil biodiversity and soil ecosystem functioning have been
1232 insufficient to date (Zeiss *et al.*, 2022) also applies to mountain soils.

1233 Direction: We support ongoing efforts (e.g. Guerra *et al.*, 2021; Arora, 2023; van der Putten *et al.*,
1234 2023) to raise the importance of soil biodiversity in environmental policies and to formulate frameworks

1235 for the protection and restoration of soils (e.g. ‘EU Soil Strategy for 2030’ and the associated ‘Soil
1236 Monitoring Law’). However, given the critical importance of healthy and biodiverse soils in mountains
1237 (e.g. for natural risk regulation), we herewith call for dedicated efforts and explicit political commitments
1238 towards their targeted protection. The ongoing development of National Biodiversity Strategies and Action
1239 Plans in response to the adoption of the Kunming-Montreal Global Biodiversity Framework represents a
1240 unique opportunity to collaborate on the formulation of soil biodiversity conservation targets and policy-
1241 ready soil biodiversity indicators applicable to mountain ecosystems, which enable policy-makers to
1242 prioritise mountain soils for conservation (Guerra *et al.*, 2021). In support of such developments, we
1243 reiterate previous calls (Maestre & Eisenhauer, 2019; Guerra *et al.*, 2021, 2022) for improved monitoring
1244 of soil biodiversity and soil-related essential biodiversity variables and for increased efforts to identify
1245 hotspots of mountain soil biodiversity and endemism, as well as priority habitats in the light of ongoing and
1246 future global change. We also call for the systematic evaluation of the efficiency of protected areas in
1247 preserving mountain soil species and their functions (see e.g. Ciobanu *et al.*, 2019). International initiatives
1248 such as SoilBON, the Global Soil Biodiversity Initiative, and the Global Soil Partnership of the United
1249 Nations Food and Agriculture Organisation represent effective opportunities for mountain soil scientists to
1250 engage with the endorsement of the Mountain Partnership (e.g. Stanchi *et al.*, 2023), the Global Mountain
1251 Biodiversity Assessment, and other institutions committed to the conservation and sustainable use of
1252 mountain biodiversity. Besides political commitments and increased scientific efforts, awareness raising
1253 and education through effective communication methods (e.g. Steinwandter & Seeber, 2022) remain
1254 essential on our path to safeguarding sustainable mountain soils.

1256 **VIII. CONCLUSIONS**

- 1257 (1) Despite a growing number of initiatives responding to the demand for data and knowledge on soil
1258 biodiversity, there are still major gaps and blind spots that exist, especially for the Global South and
1259 remote areas such as mountains.
- 1260 (2) This review intended to highlight the gaps in knowledge regarding mountains, which have become
1261 even more vulnerable due to ongoing land-use and climate change. Given the natural hazards and
1262 ecosystem services associated with mountain areas, maintaining soil health is of paramount
1263 importance. However, due to difficulties in data collection and the lack of a systematic assessment
1264 of the existing research corpus, addressing these challenges is proving challenging.
- 1265 (3) Here, we conducted a comprehensive review of the globally available data on biodiversity in
1266 temperate and continental alpine soils, above the treeline. This is, to our knowledge, the first time
1267 such data has been collated. Our systematic literature survey involved experts in the field of alpine
1268 soil biology, where we obtained an overview of the geographical distribution and number of studies
1269 focusing on alpine soil invertebrates, microbiota and cryptogams.

- 1270 (4) Our review has revealed research gaps in alpine regions outside of Europe and Central Asia, as well
1271 as for soil cryptogams and soil invertebrates, which have relatively limited data available in
1272 comparison to soil microbiota. Shortcomings were particularly notable among soil protists and soil
1273 invertebrates, and for the vast majority of uncultivated prokaryotes and fungi, for which functional
1274 or ecological descriptions are lacking. To address these issues, it will be necessary to improve
1275 geographic and taxonomic coverage. All these soil organisms have evolved over millennia to
1276 withstand the ever-growing extreme environmental conditions in mountain areas. Thus, there is a
1277 pressing need for a wider range of knowledge on all fronts.
- 1278 (5) We highlight three crucial areas for future research and policymaking on soil biodiversity in
1279 mountainous regions, emphasising their global distribution and the distinctive challenges posed by
1280 elevational gradients, remoteness and exposure to global change.
- 1281 (6) We call for a significant improvement in mountain soil biodiversity data, while we emphasise the
1282 need for enhancing the understanding of environmental drivers and consequences for biodiversity
1283 in mountain soils, advocating for improved spatial and temporal data resolution. Furthermore, we
1284 stress the importance of comparative analyses across different mountain ranges to inform
1285 conservation strategies in the face of global change.
- 1286 (7) Our review recommends clear political commitments, international collaboration, and the
1287 incorporation of biodiversity in mountain soils within global frameworks. This underscores the
1288 importance of raising awareness and providing education to promote the conservation and
1289 sustainable use of mountain soils.

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1303 X. REFERENCES

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2610 **XI. SUPPORTING INFORMATION**

2611

2612 Additional supporting information may be found online in the Supporting Information section at the end
2613 of the article.

2614 **Appendix S1:** Detailed description of the methodology and statistical analyses, accompanied by
2615 additional tables and figures:

2616 **Table S1.** List of search strings used to assess the available literature in ‘Web of Science’ focusing
2617 on alpine mountain soil biodiversity.

2618 **Table S2.** Main steps of the semi-quantitative literature analysis to assess the number of available
2619 scientific papers focusing on alpine mountain soil biodiversity.

2620 **Table S3.** List of the alpine regions and the encompassing mountain ranges used for this review.

2621 **Table S4.** Number of scientific papers focusing primarily and secondarily on cryptogams in alpine
2622 mountain soils.

2623 **Table S5.** Number of scientific papers focusing primarily and secondarily on microbiota (archaea,
2624 bacteria, fungi, and protists) in alpine mountain soils.

2625 **Table S6.** Number of scientific papers focusing primarily and secondarily on fauna (macro-, meso-,
2626 and microfauna) in alpine mountain soils.

2627 **Fig. S1.** Global map of scientific paper density per 1,000 km² on alpine soil biodiversity
2628 (cryptogams, soil microbiota and soil fauna) by mountain region.

2629 **Fig. S2.** Comparison of the area of the eleven global alpine regions used in this review.

2630