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Biodiversity in mountain soils above the treeline

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ABSTRACT

Biological diversity in mountain ecosystems has been increasingly studied over the last decade. This is also the case for mountain soils, but no study to date has provided an overall synthesis of the current state of knowledge. Here we fill this gap with a first global analysis of published research on cryptogams, microorganisms, and fauna in mountain soils above the treeline, and a structured synthesis of current knowledge. Based on a corpus of almost 1400 publications and the expertise of 37 mountain soil scientists worldwide, we summarise what is known about the diversity and distribution patterns of each of these organismal groups, specifically along elevation, and provide an overview of available knowledge on the drivers explaining these patterns and their changes. In particular, we document an elevation-dependent decrease in faunal diversity above the treeline, while for cryptogams there is an initial increase above the treeline, followed by a decrease towards the nival belt. Thus, our data confirm the key role that elevation plays in shaping the biodiversity and distribution of these organisms in mountain soils. The response of prokaryote diversity to elevation, in turn, was more diverse, whereas fungal diversity appeared to be substantially influenced by plants. As far as available, we describe key characteristics, adaptations, and functions of mountain soil species, and despite a lack of ecological information about the uncultivated majority of prokaryotes, fungi, and protists, we illustrate the remarkable and unique diversity of life forms and life histories encountered in alpine mountain soils. By applying rule- as well as pattern-based literature-mining approaches and semi-quantitative analyses, we identified hotspots of mountain soil research in the European Alps and Central Asia and revealed significant gaps in taxonomic coverage, particularly among biocrusts, soil protists, and soil fauna. We further report thematic priorities for research on mountain soil biodiversity above the treeline and identify unanswered research questions. Building upon the outcomes of this synthesis, we conclude with a set of research opportunities for mountain soil biodiversity research worldwide. Soils in mountain ecosystems above the treeline fulfil critical functions and make essential contributions to life on land. Accordingly, seizing these opportunities and closing knowledge gaps appears crucial to enable science-based decision making in mountain regions and formulating laws and guidelines in support of mountain soil biodiversity conservation targets.

Key words: alpine soils, bacteria, biogeography, cryptogams, fungi, lichens, microbial diversity, protists, invertebrates, systematic mapping.

CONTENTS

I. INTRODUCTION

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

Despite these recent developments, major gaps and blind spots still exist in soil research and in available data and knowledge on soil biodiversity. This is particularly the case for soil biodiversity in mountains (Baruck *et al*., 2016; Guerra *et al*., 2020), even though mountain soils are critical for many ecosystem processes, functions, and services, and their maintenance and stability are particularly important in terms of hazards and natural risk management (FAO, 2015; Stanchi *et al*., 2023). Given that mountain soils can take thousands of years to develop [up to 1000 years for 2–3 cm in (high) alpine areas; Stanchi *et al*., 2023], their degradation and gradual erosion as a result of overexploitation and poor management may ultimately lead to a loss of biodiversity, including locally adapted species, and to the loss of associated ecosystem functions, with no option for recovery (Körner, 2021; Singh *et al*., 2023). These threats are further exacerbated by climate and land-use change, and pollution, as well as the increasing occurrence of invasive species (Palomo, 2017; Zucconi & Buzzini, 2021; Iseli *et al*. 2023).

No work exists to date that synthesises published research on alpine soil biodiversity, takes stock of what we know, and systematically identifies gaps and biases. Here we fill this gap with an overview of current knowledge on biodiversity in mountain soils above the treeline and a semi-quantitative analysis of the state of research. In synthesising current knowledge, we particularly focus on diversity and distribution patterns, their drivers and determinants, as well as specific characteristics and adaptations. Our objectives of the latter analyses are to detect and discuss differences across taxonomic groups in (*i*) geographic hot- and blind spots, (*ii*) thematic research priorities, and (*iii*) temporal trends in research. We subsequently build on this overview to highlight opportunities for, and emerging directions of, research on mountain soils as systems of co-occurring species that interact in complex environmental matrices to fulfil various ecosystem functions (e.g. nutrient cycling), and make essential contributions to life on land (e.g. through symbiotic relationships). We restrict this review to alpine soils in temperate and continental mountain regions (Fig. 1, see online Supporting Information, Tables S1 and S3 in Appendix S1). The term 'alpine' in this context specifically refers to soils located in mountainous areas above the treeline. The work was performed as a collaborative effort by members of the Global Mountain Biodiversity Assessment (GMBA) 'Mountain Soil Biodiversity' working group. Table 1 provides a glossary of key terms used in this review.

II. METHODS AND DATA SET

(1) Expert knowledge, literature search, and text mining

A synthesis of current knowledge was prepared by 37 mountain soil biodiversity scientists from around the world, who contributed to the three main organism chapters (Sections IV–VI) according to their expertise. Information was collated in several rounds of literature searches and reviews of individual papers identified through the structured literature search detailed below. All researchers were invited to contribute insights on diversity and distribution patterns, the drivers shaping these patterns, and, if available, information on organismal adaptations, ecosystem functioning, and comparisons with global diversity trends. Given the large disparity in the information available for different groups of organisms, not all topics could be addressed in equal depth for each group.

A systematic analysis of published research was performed by querying *Web of Science* for scientific publications on mountain soil biodiversity in alpine zones (i.e. above the treeline, dark grey areas in Fig. 1) of temperate and continental climatic zones worldwide (i.e. between 23.4° and 66.6° N and S). This includes areas that according to Beck *et al.* (2023) belong to the Köppen climate categories C (temperate) and D (continental), and the high-elevation areas within temperate and continental alpine mountain ranges that belong to the tundra climate (i.e. the Köppen polar climate category ET). Therefore, we excluded studies conducted in tropical, desert and arid climates (<23.4° latitude), and arctic/polar climates (>66.6°). We did not use the Köppen classifications themselves as search terms (see Table S2).

We performed two consecutive searches, which together returned 3427 potentially relevant papers (see Appendix S1 for methodology). Using basic text-mining techniques, we searched for key terms from several hierarchically organised thesauri (including the GMBA Mountain Inventory, GADM – Global Administrative Names, BiodivThes, and EnvThes) in the title, author key words, and abstract of the selected papers (search strings are given in Table S2). Georeferencing based on extracted mountain ranges and country names allowed us to exclude publications reporting on research carried out in tropical, arid, or arctic/polar regions. We used the Global Names Finder to extract taxon names and verified these against the GBIF Backbone Taxonomy (see Appendix S1). For each publication we counted the number of appearances of these key terms by subject of interest (organismal group, mountain region, research focus, main drivers, ecosystems, etc.), and weighted these according to appearance in the title and author key words, by dividing the counts by the total number of words (which is lower in the title than in the abstract) (see Appendix S1). The weighted counts allowed us to order the subjects of interest and determine the likely primary and secondary focus of each publication regarding organismal groups, mountain regions, and research foci.

For the final analysis, this process resulted in 1380 publications (Table S3) associated with the selected organismal groups and 11 alpine mountain regions (Table S4). As some publications discussed several organismal groups and several mountain ranges, we allocated each article a primary and secondary focus based on key term/taxon counts (see above) and assigned an article to the primary alpine mountain region accordingly (see Appendix S2 and S3 for the full list of publications). We also distinguished between publications that specifically referenced taxa from one of the target organismal groups from those that only referenced a group in general terms (such as 'microbes', 'microbiota', 'invertebrates', without further details; Table 2). We assessed the accuracy of this automated classification through a random sample of 100 publications (in two subsets of 33 and one of 34 publications per organismal group) which were reviewed and validated by the lead authors. Based on this review, 14% of all the papers retained by our automatic selection approach were flagged as not entirely fulfilling all selection criteria. Among those, only three papers were misclassified, i.e. attributed to the wrong organismal groups. The remaining papers either pertained to soil biodiversity but in ecosystems such as mires or springs, to high mountain contexts not specifically above the treeline, or they pertained to the organismal group of interest only indirectly (e.g. alpine plant growth-promoting microbial traits). Accordingly, while acknowledging the uncertainty associated with automated procedures and expert validations, our comparative statistics between organismal groups, world regions, and topical focus can still be considered robust. A detailed description of the literature search and data processing methods is provided in Appendix S1, together with a list of the mountain ranges mentioned in the text.

(2) Geographic and taxonomic patterns

Out of the total 1380 publications that were retained for analysis, 517 publications had a primary focus on explicitly

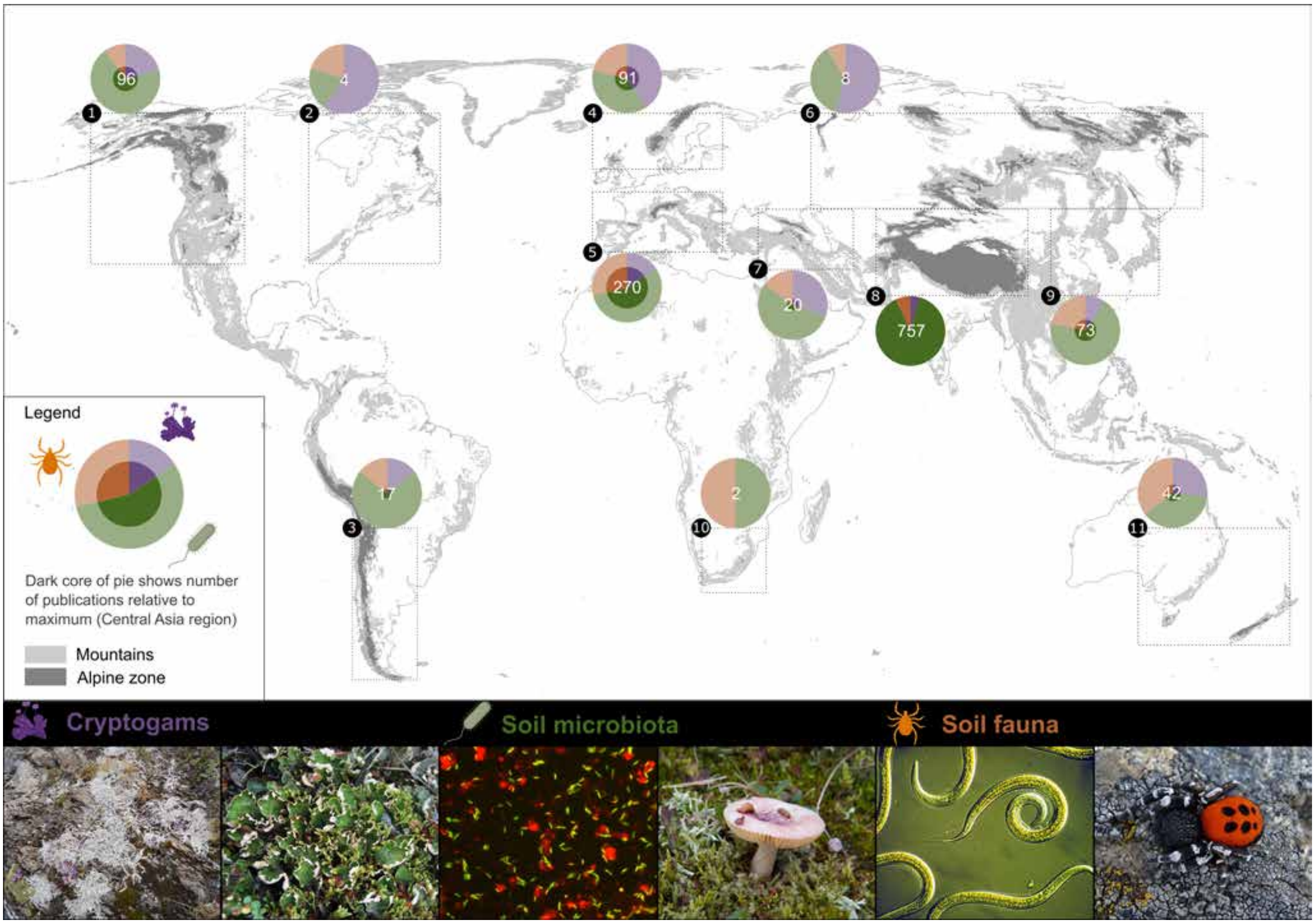


Fig. 1. Global map of the number of scientific publications on biodiversity in temperate and continental mountain soils above the treeline (cryptogams, soil microbiota, and soil fauna) by alpine mountain region. The dark core of the pies represents the number of publications in the respective area compared to the number for the region with the most publications (i.e. Central Asia). Total $N = 1380$ publications, which include all studies specifically or generically describing alpine soil biodiversity. The alpine mountain regions here are numbered as in Table S1: (1) North American Cordillera, (2) Appalachians & Northeast Ranges, (3) Andes & South America, (4) Northern Europe, (5) Central & Southern Europe, (6) North Asia, (7) Caucasus, (8) Central Asia, (9) East Asia, (10) Southern African Ranges, and (11) Australia & New Zealand. See Fig. S1 in Appendix S1 for the same data presented as density of publications per 1000 km^2 of alpine area and Fig. S2 in Appendix S1 for a visual comparison of the areas of the global alpine mountain regions discussed in this review. Icons are taken from Biorender.com. Photographs from left to right: for cryptogams: arctic–alpine lichens *Thamnolia vermicularis* (Sw.) Schaer. and *Peltigera aphthosa* (L.) Willd. (credits: Bettina Weber); for soil microbiota: DNA (green)-stained soil bacteria and soil particles (red) (credit: Nadine Praeg & Paul Illmer), *Russula* sp. (credit: Andrea J. Britton); for soil fauna: nematodes and a male velvet spider *Eresus sandaliatus* (Martini & Goeze, 1778) (credits: CSIRO Entomology and Michael Steinwandter, respectively).

named soil organismal groups (Tables 2, S3 and S5–S7). From the 1380 publications, research on soil biodiversity above the treeline is geographically concentrated in the mountains of Central Asia (Tibetan Plateau, Himalaya, Tian Shan) and Central & Southern Europe (European Alps, Pyrenees, Carpathian Mountains) (Fig. 1, Table S4). From a taxonomic point of view, 75% of scientific publications about soil biodiversity above the treeline had a primary or secondary focus on microbiota, although individual species and organismal groups were only mentioned in approximately one-third of the cases (Table S6). When focusing on primary soil taxa mentions, calculated by counts of mentions of specific taxa (e.g. *Lumbricus rubellus* Hoffmeister, 1843) or generic and broader terms (e.g. 'macroinvertebrates'), we found 1075 publications in which one of the three soil organismal groups discussed in this paper was the primary focus (Table 2, Fig. 2A). Excluding papers that referred to study taxa only generically (e.g. as 'microbes', or 'soil arthropods'), we identified 891 publications in which one of the organismal groups was the primary or secondary focus (Fig. 2B). When they are mentioned, biocrusts, micro- and mesofauna were usually the primary focus of their publications, whereas cryptogams, bacteria, and fungi are often discussed in conjunction with other organismal groups (Fig. 2B). Fungi and bacteria, for example, are often examined alongside plant communities. Soil fauna is also often discussed in relation to plant communities, although more frequently discussed on its own (Table 3).

Table 1. Glossary.

Term	Definition
Aeolian food source	Any kind of organic material that is transported by wind and that can serve as a nutrient source
Acrocarpous moss	Mosses in which the sporophyte grows at the tip of the main stem, terminating its growth (*cf.* pleurocarpous moss)
Autotrophic	Ability to produce biomass solely by using inorganic substances; often refers to carbon-autotrophy when using inorganic carbon compounds, such as CO_2, for synthesis of biomass-carbon
Brachyptery	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	Non-vascular plants that include mosses, hornworts, and liverworts
Cetrarioid lichen	Monophyletic group of lichens that either belong to or are closely related to the genus *Cetraria*
Chionophilous	Organisms that prefer or need a permanent snow cover
Chionophobic	Organisms that avoid snow-covered habitats
Cryophilous	Organisms that prefer very low temperatures
Cryptogams	Organisms that do not form flowers and seeds but reproduce by fission, fragmentation, and spores
Ecotone	Transition between ecological communities, ecosystems, and/or ecological regions along an environmental gradient
Endemic	Native and restricted to a certain geographic area
Endophyte	Organisms, mostly fungi or bacteria, living within a plant without causing a disease
Epiphyte	Growing on plants
Eukaryotes, eukaryotic/eukaryote	Organisms with a cell nucleus (protists, animals, fungi, plants)
Euryhydric	Ability to withstand a wide range of humidity
Fellfield	Alpine tundra regions characterised by frequent freeze–thaw cycles due to the harsh climate, dry, shallow soils, and sparse cover of characteristic vascular plants
Ground-dwelling	Soil animals that live primarily on or near the ground (i.e. surface)
Fruticose	Lichens with a three-dimensional, shrub-like or bushy growth pattern
Liverwort	A non-vascular bryophyte that belongs to the division Marchantiophyta
Microbiota	Prokaryotes (archaea, bacteria), fungi, protists, and viruses
Nitrogen fixation	Here referring to biological nitrogen fixation – the energy-consuming process by which N_2 is converted to NH_3; only performed by bacteria and archaea
Nunatak	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	Organisms that favour rocky environments
Pleurocarpous moss	Mosses in which the sporophyte is borne on short lateral branches and not terminating the growth of the main axes (*cf.* acrocarpous moss)
Poikilohydric	Organism whose water content is passively controlled by the environment
Prokaryotes, prokaryotic/prokaryote	Organisms without a cell nucleus (archaea and bacteria)
Protists	All eukaryotes that are not plants, metazoans, or fungi
Rhizosphere	Narrow space/region in the soil directly influenced by plant roots
Saprotrophic	An organism that feeds on dead organic matter
Saxicolous	Growing on rock
Terricolous	Growing on soil

Table 2. Focus and taxonomic specificity of scientific publications on mountain soil biodiversity above the treeline included in this review. The numbers do not sum correctly because other taxa (plants or vertebrates) could be the primary or secondary focus of studies on soil biodiversity but are not included in this review.

Focus	Specific (e.g. fungi, microfauna)	Generic (e.g. microbes, soil arthropods)	Either
Primary	517	624	1075
Secondary	455	370	739
Either	891	991	1380

Over the past 25 years, the volume of published scientific literature on soil biodiversity above the treeline has grown considerably, with a clear acceleration after 2010 (Fig. 3). Temporal trends vary among organismal groups, with a particularly steep increase over the last decade in research on soil bacterial and fungal communities, followed by micro-, meso-, and macrofaunal research (Fig. 3). Soil protists remain comparatively understudied. There has been a gradual increase in research focusing on biocrusts. Compared to other organismal groups, cryptogams, fungi, and macrofauna already had a relatively high number of publications by the year 2000, reflecting an early focus of mountain soil ecosystems research.

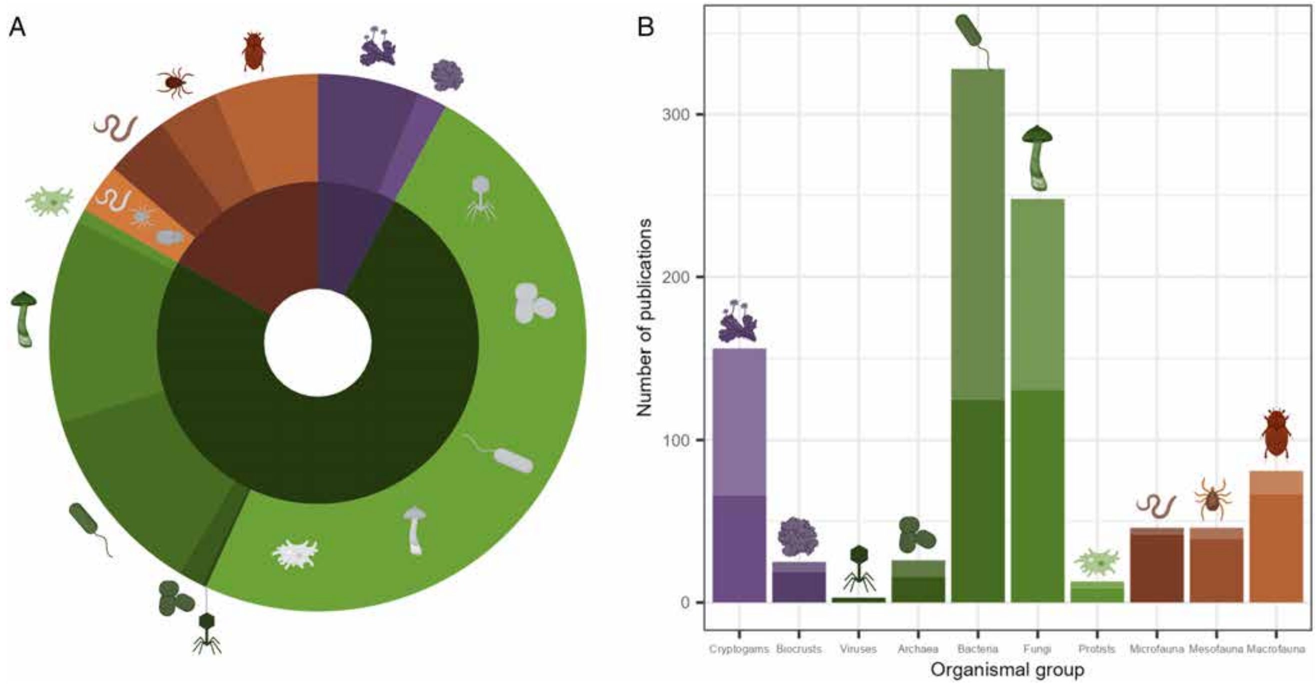


Fig. 2. (A) Number of scientific publications with a primary focus on one of the three alpine soil organismal groups discussed in this review: biocrusts and other cryptogams; soil microbiota (viruses, archaea, bacteria, fungi, and protists); and soil fauna (micro-, meso-, and macrofauna). The counts include publications applying generic terms with no explicit mentions of specific species or organismal groups (e.g. 'microbes', 'arthropods': indicated with grey icons). (B) Number of publications with a primary or secondary focus on these organisms but excluding publications using only generic organismal terms. The darker base of the bars indicates the number of publications where that group is the primary focus, the lighter part where it is the secondary focus. Icons are taken from Biorender.com.

III. MOUNTAIN SOILS ABOVE THE TREELINE

(1) Soil properties and drivers

According to the Keys to Soil Taxonomy (Soil Survey Staff, 2022), major soil types occurring in the alpine and nival zones of temperate and continental mountains include entisols, inceptisols, mollisols, histosols, gelisols, and spodosols. Soil formation in mountain areas is typically controlled by climatic factors, microrelief and morphodynamics, gravitational and fluvial dynamics, solifluction, and wind-related processes (Egli, Dahms & Norton, 2014). Accordingly, soil types and properties show small-scale heterogeneity (Egli & Poulenard, 2016) resulting from high variability in these controlling factors (Burga, Klötzli & Grabherr, 2004a; Hoorn,

Table 3. Percentage of scientific publications on alpine soil biodiversity where the main soil organismal groups (cryptogams, microbiota, fauna) are a primary (rows) *versus* secondary (columns) focus of the study. Publications discussing the diversity of plants and vertebrates in alpine soils are only included when one of the focal soil organismal groups (cryptogams and biocrusts, soil microbiota, soil fauna) was also analysed (hence they are shown in parentheses). For example, microbiota ($N = 810$ studies in total) were discussed alone in 28% of publications (e.g. publications on fungi), in 39% one taxonomic group of microbiota was discussed alongside another group of microbiota (e.g. fungi and bacteria), and in 31% of the publications on a microbiota group, plants were also discussed.

		Secondary focus						
		Alone	Cryptogams	Microbiota	Fauna	(Plants)	(Vertebrates)	Total number of studies
Primary focus	Cryptogams	27%	11%	31%	0%	32%	0%	**85**
	Microbiota	28%	1%	39%	0%	31%	1%	**810**
	Fauna	31%	2%	10%	31%	23%	3%	**180**
	(Plants)	0%	24%	68%	7%	0%	0%	**298**
	(Vertebrates)	0%	14%	29%	43%	14%	0%	**7**
								1380

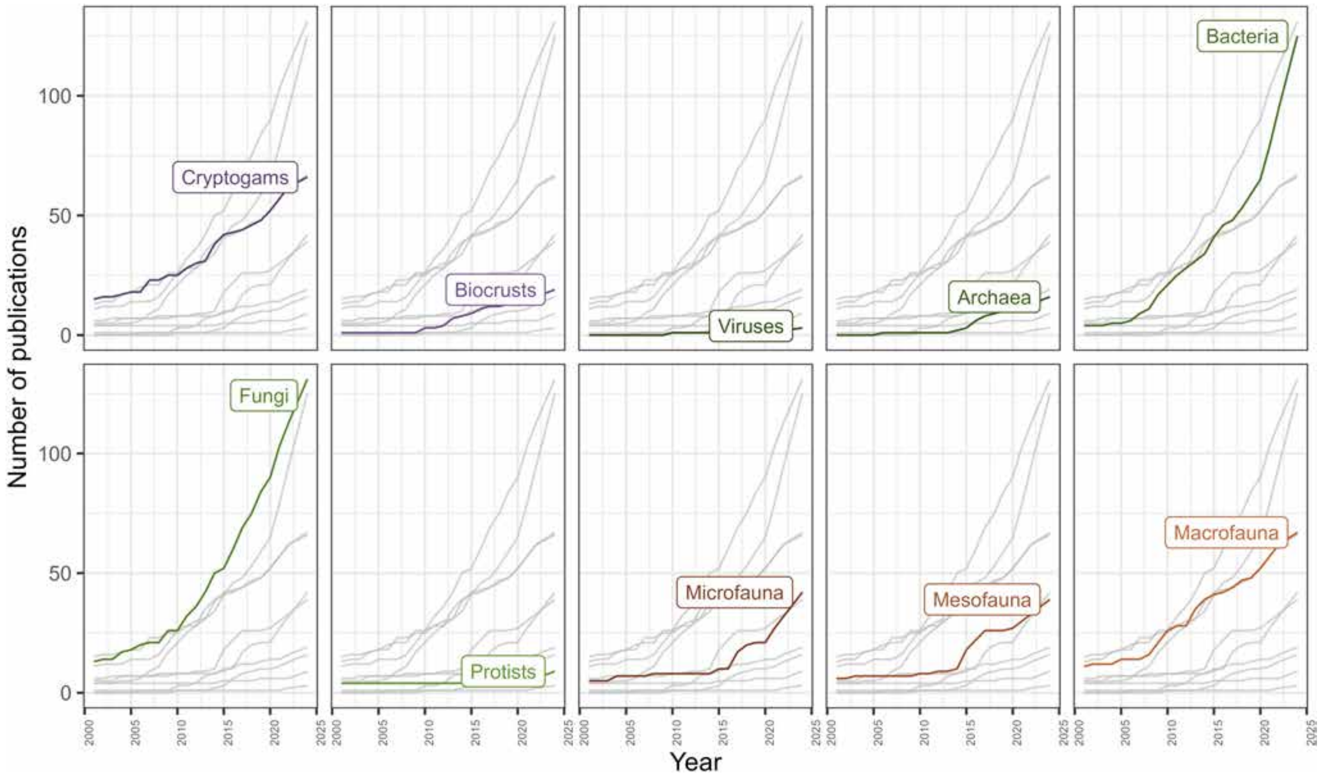
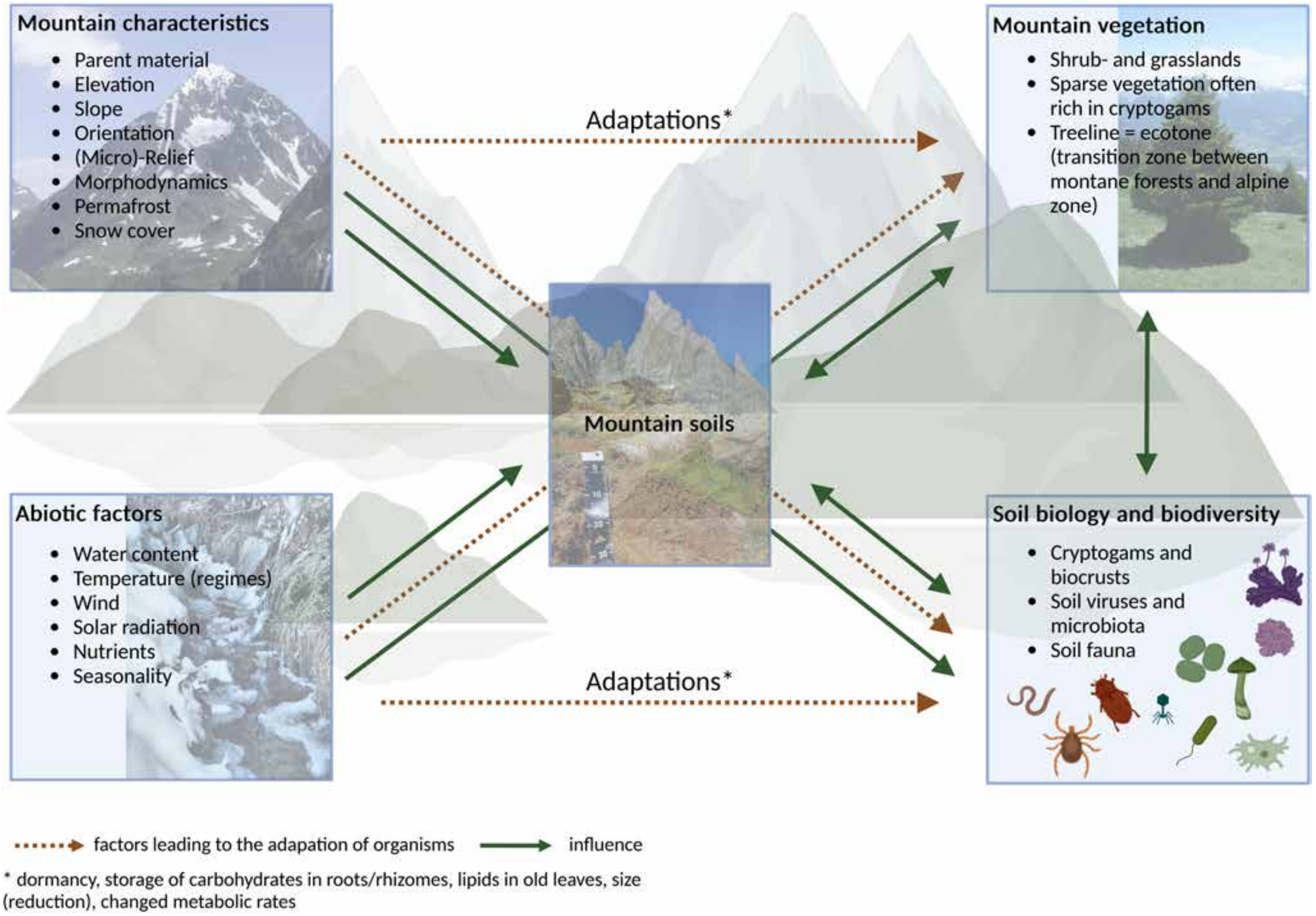


Fig. 3. Line graphs showing the cumulative number of scientific publications through time dealing with soil biodiversity above the treeline in temperate and continental mountain regions. The numbers represent the publications with a primary focus on the specific alpine soil organismal groups shown.

Perrigo & Antonelli, 2018). Properties that are specific to alpine soils include an incomplete development (Donhauser & Frey, 2018), with slow humus accumulation and limited nutrient supply, even though accumulation of wind-blown fine material may improve the physical and chemical characteristics of stony substrates on a small scale (Gild, Geitner & Sanders, 2018). Detailed information on mountain soil types and characteristics is an important prerequisite to understanding biodiversity in soil and the unique adaptations of soil organisms (Fig. 4) (Pellissier *et al.*, 2014; Orgiazzi *et al.*, 2016; Yashiro *et al.*, 2016; Mod *et al.*, 2020; Seppey *et al.*, 2020). However, this information remains rare (Baruck *et al.*, 2016; Guisan *et al.*, 2019) and relies on specific and targeted initiatives (e.g. establishment of the 'Alpine Soil Partnership' in 2017).

Generally, life in mountain soils is determined by their abiotic properties. These include water content and temperature as the main drivers of chemical and physical weathering, and the quality and quantity of organic matter. The parent material, including its chemical composition and physical properties, its resistance to weathering and its predetermination of soil pH, also plays an important role (Fig. 4) (Paul & Clark, 1996). Typically, there is a close correlation between the content of organic matter and the degree of plant cover or the formation of plant biomass, which generally leads to a decrease in organic matter content with increasing elevation (Winkler *et al.*, 2018; Praeg, Pauli & Illmer, 2019). Thus, nival and alpine soils usually exhibit minimal carbon stocks (Frey *et al.*, 2016; Adamczyk *et al.*, 2019; Luláková *et al.*, 2019) compared to soils at lower elevations, where temperatures and plant coverage are higher, and which therefore may act as larger carbon sinks. Yet, this relationship between carbon content and elevation is not always linear, and various factors can modify the general pattern. It has, for instance, been shown that cold and wet conditions, along with the associated reduction in the decomposition of organic matter, can lead to a local increase in carbon content (Praeg *et al.*, 2020), and windborne inputs at higher elevations can contribute locally to an elevated organic matter content. Mountain regions have received increasing attention for their contribution to terrestrial carbon (C) storage (Hagedorn, Gavazov & Alexander, 2019; Stanchi *et al.*, 2021), specifically in the context of climate change (Walker *et al.*, 2022).

Drivers of change in soil abiotic properties are numerous but in many mountain regions, an important one is winter sports. Activities such as the establishment and maintenance of (large) ski areas, including levelling and grading operations, represent strong mechanical disturbances. These disturbances promote the breakdown of soil aggregates, cause the exposure of organic matter that was previously protected in undisturbed soils (Gros *et al.*, 2004), and promote soil



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

Fig. 4. Overview of mountain characteristics and abiotic factors influencing the alpine landscape, mountain soils, and alpine soil organisms. Icons are taken from Biorender.com. Photograph credits: Paul Illmer, Nadine Praeg, Michele D'Amico, Emanuele Pintaldi.

erosion. Together, these impacts lower the organic carbon content (Delgado *et al.*, 2007; Negro *et al.*, 2013) and reduce the soil micropore porosity, with consequences for soil aeration and water-holding capacity (Pohl *et al.*, 2009). Additionally, artificial snowmaking uses nucleating agents and water, often diverted from lakes and streams, which contain mineral and organic compounds that are not present in natural snow. This provides an additional input of solutes during snow melting (Wipf *et al.*, 2005; Roux-Fouillet, Wipf & Rixen, 2011), resulting in higher soil pH and electrical conductivity (Delgado *et al.*, 2007; Freppaz *et al.*, 2013; Casagrande Bacchiocchi *et al.*, 2019).

An additional factor affecting life in mountain soils is the presence of a substantial and long-lasting snow cover. Together, seasonal snowpack depth, duration, and melt-out control the onset and duration of the growing season, mitigate low soil temperatures, and affect microbial activity, soil nutrient cycling, soil gas fluxes, and pedogenesis (Freppaz *et al.*, 2017). These factors further determine community composition, and their high spatial variability may enable the close co-occurrence of species adapted to different environmental conditions, such as chionophilous and chionophobic taxa (Odland & Munkejord, 2008; Carlson *et al.*, 2015; Niittynen & Luoto, 2018; Seeber *et al.*, 2021; Panchard *et al.*, 2023). Considering the impact of global change, mountain soils are likely to undergo major transitions connected with higher temperature, more rain and less snow, and a distinct disturbance of permafrost systems. However, changes will not follow a predictable trajectory but will lead to different responses (Ernakovich *et al.*, 2014; Knight, 2022). Given the fluctuating soil and climate influences (e.g. low temperatures, freeze–thaw cycles, wet and dry conditions) and short growing seasons of alpine regions, there are likely brief periods of biogeochemical activity where seasonal pulses of nutrients and plant phenology promote or deter belowground processes (Kuzyakov & Blagodatskaya, 2015). With climate warming, nival soils can be expected to serve increasingly as carbon sinks but they are equally expected to become nitrogen sinks due to increased plant productivity under warmer conditions (Steinbauer *et al.*, 2018). This holds especially true for barren or sparsely vegetated soils with low carbon and nitrogen content, where increased plant growth and primary production clearly outweigh temperature-driven increases in soil respiration (Hagedorn *et al.*, 2019).

By contrast, distinct increases in carbon loss have also been reported as a consequence of increased temperatures allowing lowland plants to colonise alpine environments (Walker *et al.*, 2022). Soil microbial activity persists throughout the year but is closely linked to temperature as well as the timing and quantity of snowfall and snowmelt (Ernakovich *et al.*, 2014). In alpine ecosystems, warmer summer temperatures will thaw seasonally frozen ground, enhancing the availability of organic carbon for microbial decomposition. Projected climate change-related shifts are thus expected to alter microbial activities, communities, and nutrient dynamics (Ernakovich *et al.*, 2014), and to change the coupling of above- and below-ground processes (Broadbent *et al.*, 2024). Thus, predictions about the amount and dynamics of carbon and nitrogen cycling in response to global warming can only be made on the basis of a better understanding of the complex biotic and abiotic interactions in mountain soils (Fig. 4).

(2) Vegetation

Soil types and properties are also key in determining vegetation distribution in the alpine zone. Between the treeline and the zone of perennial snow and ice, alpine vegetation consists of shrub- and grasslands that gradually give way to high alpine vegetation dominated by species-rich cryptogam communities. The treeline itself is a transition zone, a so-called ecotone, between the higher montane and subalpine forest, often dominated by coniferous trees, and the alpine zone.

The abundance of plant species and their distributions are determined by temperature, water availability, and the duration of snow cover, which results from the interacting effects of temperature, precipitation, topography, and wind (Rodwell, 1992a,b; Thompson & Brown, 1992; Panchard *et al.*, 2023). Alpine grasslands share many structural and functional traits and characteristics with polar grass-dominated tundra ecosystems (Riebesell, 1982; Janišová *et al.*, 2011; Dengler *et al.*, 2014), and in both systems, low air and soil temperatures, including frost, and the duration and/or lack of snow cover are important constraints on plant growth. Permafrost (i.e. continuous frost conditions), in turn, controls the entire soil system and slows down all biotic activity (Parolo & Rossi, 2008; Zollinger *et al.*, 2013; Goordial *et al.*, 2016; Giaccone *et al.*, 2019; Jin *et al.*, 2021). At the upper limit of grasslands, occasional increases in aridity and shortened vegetation periods cause poikilohydric cryptogamic organisms gradually to replace the standing euryhydric seed plants (Körner, 2021).

Adaptations of alpine vegetation to short and cold growing seasons include the ability to metabolise rapidly at low temperatures, the transition to dormancy as a strategy to withstand the rigours of winter, and the storage of carbohydrates in roots/rhizomes or of lipids in old leaves for regrowth and flower primordia formation (Billings, 1974) (Fig. 4). Alpine plants are also adapted to intense solar radiation, as well as to extended periods of dehydration. While the structure and composition of alpine vegetation depends on soil type and the chemical and physical properties of soil, plant communities, in turn, influence soil structure, properties, and stability.

IV. CRYPTOGAMS AND BIOLOGICAL SOIL CRUSTS

Key messages: 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 first increase above the treeline and then decrease towards the nival belt, but at slower rates than that of vascular vegetation. The composition of lichen and to a lesser extent bryophyte communities is strongly related to bedrock chemistry and soil texture. Climate change results in the upwards migration of bryophytes, whereas at lower elevations sensitive and rare lichens and bryophytes are endangered by seed plant (over)growth. We found 85 publications dealing primarily and 96 dealing secondarily with alpine cryptogams (i.e. 25 for biological soil crusts and 156 for cryptogams), mainly from the alpine mountain regions of Central & Southern Europe (28.2%), Northern Europe (21.0%), and Central Asia (18.8%); see Fig. 5 and Table S5.

(1) Cryptogams

(a) *Brief introduction of organismal group*

Cryptogams are mostly non-vascular organisms (ferns, which are vascular cryptogams, were not included here) that do not form flowers and seeds but reproduce by fission, fragmentation, and spores. They do not represent a monophyletic group, as they comprise lichens, bryophytes, eukaryotic algae, and cyanobacteria (Büdel, Friedl & Beyschlag, 2024). Cryptogams occur widely at different elevations in alpine regions, where they grow epiphytically on vascular plants as well as on and within rocks (saxicolous) and on soil. In some cases, soil-inhabiting organisms form biological soil crusts (abbreviated as biocrusts). Since biocrusts are defined as an 'intimate association between soil particles […] and organisms which live within, or immediately on top of, the uppermost millimetres of the soil' (Weber *et al.*, 2022, p. 1781), they do not include fruticose lichen and bryophyte carpets, which mainly grow above the soil and form valuable vegetation components on their own. A detailed description of alpine cryptogamic organisms occurring in biocrusts is given in Section IV.2 below, other cryptogams occurring on and in soil are included in this section.

Recent and historic species collections are often restricted to a given research site, striving for a thorough assessment of all species growing there. Today, species collections are often accompanied by quantification of environmental variables, such as soil parameters and climate data, to characterise the microhabitats inhabited by cryptogams (Miller, 2009; Sun *et al.*, 2013; Vanneste *et al.*, 2017; Mejia *et al.*, 2020). Specimens that originate from fieldwork are kept in herbaria

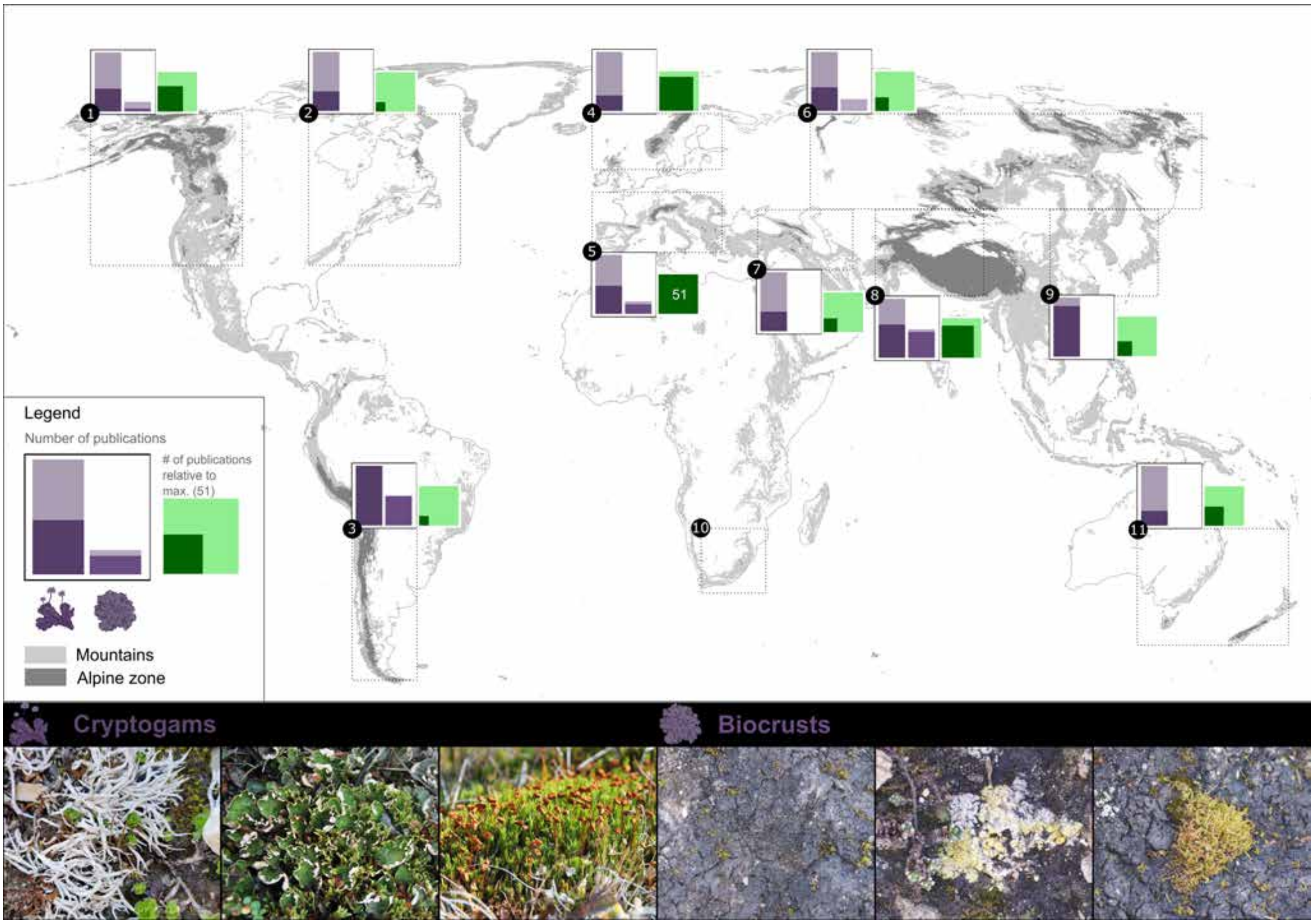


Fig. 5. Global map of the number of scientific publications on cryptogam biodiversity in temperate and continental mountain soils above the treeline by alpine mountain region. Number of publications is given per crust type and relative to the maximum number of publications found (Central & Southern Europe, *N* = 51): the dark-coloured part of the bar represents those publications in which this group was deemed the primary focus, the light-coloured part represents those publications where this group was the secondary focus. See Appendix S1 for a detailed description of the methods and Table S5 for publication numbers per alpine mountain region and soil organismal group. Icons are taken from Biorender.com. Photographs from left to right: for cryptogams: arctic–alpine lichen *Thamnolia vermicularis* (Sw.) Schaer., alpine zone of the Großglockner, Austria (credit: Stefan Herdy); arctic–alpine lichen *Peltigera aphthosa* (L.) Willd. and arctic–alpine moss *Polytrichum* sp. in vicinity of Kangerlussuaq, Greenland (credit: both Bettina Weber); for biocrusts: cyanobacteria-dominated soil crust (dark surface colouration) intermingled with bryophytes; cyanobacteria-dominated biocrust mixed with chlorolichens, dominated by *Fulgensia* sp.; cyanobacteria-dominated biocrust mixed with mosses, dominated by *Tortella* sp. (all three from the alpine zone of the Großglockner, Austria; credits: Stefan Herdy).

and are identified using monographs, cryptogam floras or determination keys in combination with microscopy or chemical methods (Bergamini, Ungricht & Hofmann, 2009; Sun *et al*., 2013; Mejia *et al*., 2020). For mapping and coverage analyses, species distributions are assessed using quadrats (mostly 25 cm × 25 cm in size) or plots (1 to few m^2), where the dominant vegetation or community composition can be monitored over time (Miller, 2009; Sun *et al*., 2013; Vanneste *et al*., 2017; Mejia *et al*., 2020).

(*b*) *Geographic focus and diversity*

Cryptogam diversity studies are concentrated in Europe (49.2% of studies with cryptogams as primary or secondary focus; Fig. 5, Table S5), followed by Central Asia (18.8%). In Europe, descriptions exist for 200 lichen species in the nival belt of the Alps, with a remarkable development of the genera *Cetraria*, *Parmelia*, and *Umbilicaria* (Ozenda & Borel, 2003). The number of bryophytes and macrolichens increases towards the north, with 150–200 species of lichens in the Pyrenees (Gómez, Sesé & Villar, 2003), 65 bryophyte and 218 lichen species in the south-eastern Carpathian Mountains (Coldea, 2003), 439 species of bryophytes in the Italian Alps (Pedrotti & Grafta, 2003), and about 558 bryophyte species in the Southern and Northern Scandes (Virtanen *et al*., 2003). However, these species numbers will depend on the intensity and quality of biodiversity assessments and the availability of appropriate tools for species recognition (e.g. Nimis & Martellos, 2004). Moreover, publications often do not mention the number of terricolous species found above the treeline. Precise data are thus hidden in the literature, unless floristic information is directly searchable in a database. A search for soil-inhabiting lichens present in Italy using the Italic database (https://italic.units.it/ ; Nimis, Conti & Martellos, 2024) retrieved 296 taxa above the treeline (one-third of which were foliose or fruticose). Areas with the highest species richness of bryophytes and the highest numbers of threatened species are located in the eastern European Alps, Carpathian Mountains, eastern Pyrenees, and the Scandes in Northern Europe (Hodgetts *et al.*, 2019). The highest elevational records for lichens and bryophytes are from the subtropical Dry Andes in South America, near the summit of Socompa volcano at 6060 m (Halloy, 1991), and on Mount Everest, Himalaya at 7400 m [*Lecidea vorticosa* (FLÖRKE) KÖRB. and *Pertusaria bryontha* (ACH.) NYL.; Miehe, 1988].

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

(*c*) *Drivers and interactions*

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

In temperate Central European mountains, alpine grasslands are characterised by the presence of large meadows dominated by genera including *Festuca* and *Carex* (Ozenda, 1988), driven by the presence of a long-standing, deep snow cover, which melts relatively rapidly in spring. In this region, communities dominated by bryophytes and lichens cover only relatively small areas. By contrast, in Central Asian and Scandinavian mountains, higher aridity or a stronger clearing of snow cover by wind promotes communities richer in cryptogams and less dominated by graminoids. This trend is also observed in continental Nearctic mountain ranges such as the Rocky Mountains (Leuschner & Ellenberg, 2017). In all mountain ranges, snow abrasion poses a major mechanical challenge to alpine vegetation of exposed habitats (Wieser, Holtmeier & Smith, 2014) and promotes the development of stress-tolerant cryptogamic communities in windswept localities.

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

The species composition of lichen communities varies significantly, depending on the bedrock chemistry and resulting texture of the mineral fraction of local soils (Guo & Cao, 2001). Calcium-rich spring seeps were observed to form refugia harbouring a rich variety of bryophytes and lichens (Miller, Fryday & Hinds, 2005). Conversely, areas with higher water retention and permanently flooded soils develop into bryophyte-dominated bogs mostly shaped by *Sphagnum* species and pleurocarpous mosses (Halsey, Vitt & Gignac, 2000; Wahren, Williams & Papst, 2001b; Bragazza, Gerdol & Rydin, 2003). On wet soils and snowfields with a long snow-cover duration, cryptogams can reach high diversity (Dierssen & Dierssen, 2005; Cooper *et al.*, 2010). In alpine fellfields, cryptogams are a prominent component, with lichens covering up to about 50% of the surface area on the Beartooth Plateau, Montana and Wyoming (Greater Yellowstone Rockies; Eversman, 1995).

Generally, lichen communities develop on substrates with little mechanical perturbation under changing hydration conditions. Wet and soft soils of glacier forefields are not colonised by lichens. Soils in many windswept localities are typically colonised by fruticose lichens, which usually interlock with shrubby plants rather than being connected with the soil. In contrast to the common notion of lichens as pioneer vegetation, crustose lichens in biocrust communities need not only soil stability but also long stable time intervals to develop, and they can suffer local extinction due to shading from nearby plants (Schellenberg & Bergmeier, 2020).

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

Interactions between plants and lichens have also been explored (Favero-Longo & Piervittori, 2010). Most notably, the elimination of fruticose lichens, especially cetrarioid species, has been shown to significantly reduce the growth of neighbouring grasses and sedges (Jespersen, 2013), probably as a result of changes in microclimate, surface water retention, and protection from run-off. In an experimental approach, presence of most lichens facilitated seedling recruitment, while only very thick mats of *Cladonia stellaris* (Opiz) Pouzar & Vězda had an inhibitory effect (Nystuen *et al*., 2019). Similarly, *Racomitrium lanuginosum* Bridel mats stimulated growth of the sedge *Carex bigelowii* Torr. ex Schwein. in the alpine subarctic tundra of Swedish Lapland (Rago/Skjomfjellet, Northern Scandes; Carlsson & Callaghan, 1991).

One means by which evolution has made it possible for lichens and mosses to overcome competition with seed plants or unsuitable soil conditions is by the development of shrub-like fruticose morphologies, which grow as lichen heath and pleurocarpous mosses between persistent seed plant vegetation such as dwarf shrubs (e.g. genera *Vaccinium*, *Salix*, and *Erica* with *Hypnum cupressiforme* Hedw.; Schellenberg & Bergmeier, 2020).

(*d*) *Environmental change effects*

Effects of environmental changes on cryptogams are diverse. Climate change in alpine regions generally causes a shift of bryophytes to higher elevations (Wen *et al*., 2022), whereas nutrient input, CO_2 increase or warming cause vascular plant productivity to increase at the cost of sensitive and long-established soil lichen and bryophyte communities (Graglia *et al*., 2001; Klanderud, 2008; Dawes *et al*., 2017). Such changes in plant communities also affect microbial community composition, which may result in altered biogeochemical cycling (Bueno de Mesquita *et al*., 2017). In Switzerland, climate change appears associated with an increase in the mean elevation of bryophytes, which is likely due to an upward shift of their upper range limits as well as to the extinction of cryophilous species at lower elevations (Bergamini *et al*., 2009). Changes in bryophyte and lichen species richness, cover, and composition were also observed during a 15-year period from 2001 to 2015 in the Southern Scandes of Norway, with an effect on species interactions. For lichens, the observed decrease in species richness and cover over time was attributed to increased competition with vascular plants (Vanneste *et al*., 2017).

Anthropogenic drivers, such as grazing, trampling, and nitrogen deposition also affect cryptogams in complex and multiple ways. For instance, the effects of grazing are variable. Grazing in extensively farmed secondary grasslands has been shown to increase the diversity and coverage of bryophytes and lichens due to decreased competition for light (Nascimbene, Fontana & Spitale, 2014). On the other hand, in mid-elevation pastures (3000–3400 m) in India (Gangotri Group, Himalaya), where the landscape is dominated by open alpine grasslands with grazing pressure usually at its peak, lichen diversity is reduced compared to higher (3400–4000 m) and lower (2700–3000 m) habitats where less pastureland is available, or soil cover becomes scarce (Rai *et al*., 2012). In the Uinta Mountains of Utah (Western Rocky Mountains), grazing favoured the growth of crustose or squamulose lichens, whereas in ungrazed areas fruticose and foliose taxa also occurred (St. Clair *et al*., 2007). Seed plants are also affected, since further effects of (heavy) grazing include an increase in root biomass (Mayel, Jarrah & Kuka, 2021), also in alpine meadows (Yang *et al*., 2018), likely resulting from increased rates of nutrient cycling due to herbivore excretion. The effects of trampling include the reduction of lichen abundance and diversity in an alpine heath ecosystem (Jägerbrand & Alatalo, 2015) as well as a reduced coverage of the moss *Pleurozium schreberi* (Willd. ex Brid.) Mitt. in a subarctic grassland in northern Sweden (Rago/Skjomfjellet, Northern Scandes; Sørensen *et al*., 2009).

Finally, existing evidence for the effects of nitrogen deposition on cryptogams includes a loss of moss cover in alpine *Racomitrium* moss–sedge heath in the UK (Britton *et al*., 2018), along with a general decline in richness and a community shift from bryophytes and lichens towards graminoids (Nilsson *et al*., 2002; Armitage *et al*., 2014; Britton *et al*., 2019). Declines in moss cover are possibly due to the positive effects of nitrogen deposition on the growth of saprotrophic fungi associated with moss necromass; this likely causes the reduction in the thickness and cover of the moss carpet and enables graminoids to outcompete mosses (Taylor *et al*., 2022). In a study in Norway, nitrogen addition caused a decrease in lichen cover and size (Fremstad, Paal & Mols, 2005), whereas in northern Sweden, nitrogen, phosphorus, and potassium fertilisation positively affected bryophyte biomass (Haugwitz & Michelsen, 2011).

After disturbance, succession under natural conditions or facilitated by restoration measures may help to restore the natural vegetation state. In a study investigating succession on soil heaps left after construction/soil excavation in alpine sites in western Norway (Southern Scandes), it took about

30 years for the bryophyte and lichen cover and species richness to approach that of the surrounding area (Rydgren *et al.*, 2011). Comparable results were also obtained in a separate study, where gamma diversity of cryptogams peaked 23–28 years after cessation of ploughing and fertilising of subalpine grasslands (Austrheim & Olsson, 1999). In a study on habitat restoration after clearcutting of non-indigenous *Pinus mugo* TURRA in the Eastern Sudetes (Bohemian Massif), bryophyte diversity was mapped and compared to that in areas of undisturbed dwarf pine canopy and in autochthonous grassland areas. The results revealed habitat homogenisation, as related to bryophytes, 9 years after the impact, and suggested that restoration measures, in addition to clearcutting, might be helpful to enhance restoration speed and quality (Zeidler *et al.*, 2022). In a different study in arctic sites in Iceland, application of shredded turf led to a rapid increase in bryophyte cover and thus might represent a valuable restoration measure (Aradottir, 2012).

(2) Biocrusts

(*a*) *Brief introduction of organismal group*

As a pioneer community in alpine environments, biological soil crusts (biocrusts) comprise a dense layer of cyanobacteria, green algae, lichens, and bryophytes that covers the soil surface (Gold, Glew & Dickson, 2001; Huber *et al.*, 2007; Karsten & Holzinger, 2014; Mikhailyuk *et al.*, 2015; Weber, Büdel & Belnap, 2016) and grows in patches between seed plants (Türk & Gärtner, 2003). Unlike lichen and bryophyte carpets, biocrusts do not elevate much above the soil surface. However, their presence and activity play a crucial role in forming soil aggregates, thereby enhancing soil stability. Early successional communities are dominated by cyanobacteria, which facilitate gradual colonisation by lichens and bryophytes under suitable conditions. A more detailed definition of biocrusts and their delimitation against other cryptogam communities was published by Weber *et al.* (2022). While it is true that biocrusts also host a wealth of different bacteria, fungi, viruses, and mesofauna (Weber *et al.*, 2022), the state of knowledge on these organism groups in alpine biocrusts is still too incomplete to cover them here in further depth. Instead, these organism groups are covered in general (and not related to biocrusts) in Sections V.1–3, and VI.2.

Biocrusts provide ecosystem services *via* their functions in soil stabilisation, nitrogen and carbon fixation, nutrient accumulation, and water retention (Gold *et al.*, 2001; Huber *et al.*, 2007; Peer, 2010; Zheng *et al.*, 2014a; Jung *et al.*, 2018; Borchhardt *et al.*, 2019). They are further known for improving soil microenvironments, mainly due to the activity of microorganisms within the biocrust (Wei *et al.*, 2022a). In the case of glacier forefields, cyanobacteria fix and thus provide nitrogen to the strongly N-limited raw soils, with rates directly related to the availability of organic carbon (Wang *et al.*, 2021c). High nitrogen-fixation rates by alpine *Collema*-dominated biocrusts in the mountains of Western Canada [i.e. Chilcotin Plateau (British Columbia Interior) and Southern Icefield Ranges (Saint Elias Mountains)] suggest an important contribution of cyanolichens to ecosystem nitrogen budgets (Marsh *et al.*, 2006). While Antarctic and alpine biocrusts show similarities in species composition, alpine biocrusts seem to be much more physiologically active than their polar counterparts (Colesie *et al.*, 2014, 2016), with activity rates closely linked to the local climatic conditions (Raggio *et al.*, 2017). Methods of biocrust sampling and analysis vary depending on the research question, with sampling being either conducted in certain spots (if particular biocrust types are of interest), along a transect (if a gradient is studied), or randomly (if coverage and composition are analysed) (Řeháková, Chlumská & Doležal, 2011; Jung *et al.*, 2018; Rodríguez-Caballero *et al.*, 2022). Sampling itself is either conducted with a spatula, or with sampling vessels, like petri dishes, which are pressed upside down into the soil and then lifted together with the biocrusts, using a spatula (Dojani *et al.*, 2014). Biocrust analysis is conducted by means of morphological determination, applying microscopy and cultivation of biocrust components (e.g. cyanobacteria) and increasingly by molecular genetic analysis, which can also be used to identify heterotrophic biocrust components (Řeháková *et al.*, 2011; Dojani *et al.*, 2014).

(*b*) *Geographic focus and diversity*

Our global literature assessment showed that biocrusts are rarely the primary research focus of mountain soil biodiversity studies, and there is a lack of biocrust studies for entire mountain ranges worldwide (Fig. 5, Table S5). For most biocrust studies, a secondary focus of the study is usually present (Fig. 5).

Whereas cryptogams occur widely in alpine grasslands, biocrusts are mainly restricted to the high alpine zone, where they can achieve considerable coverage. In the Austrian Alps (Hochtor, High Tauern), for example, biocrust coverage reached up to 30% of the surface area (Büdel *et al.*, 2014), with a high prevalence of cyanobacteria, which has also been observed in Himalayan soils (Řeháková *et al.*, 2011). An increase of cyanobacterial biomass with elevation was also detected for cyanobacteria-dominated biocrusts in the Zanskar Range (Himalaya; Janatková *et al.*, 2013).

(*c*) *Drivers and interactions*

The occurrence and composition of biocrusts in alpine regions appear to be influenced mainly by habitat availability and precipitation (Büdel *et al.*, 2009; Lütz, 2012; Jung *et al.*, 2018; Xiao *et al.*, 2020a). Biocrust activity status, in turn, is regulated by morphological, physiological, and local microclimatic conditions (Longton, 2009; Tamm *et al.*, 2018). Additional variables affecting biocrust occurrence include elevation, aspect, snowpack, dust input in alpine areas, as well as standing vegetation (Miller, 2009; Sun *et al.*, 2013; Mejia *et al.*, 2020; Peer *et al.*, 2022). Across four mountain ranges at high elevation in Ladakh, India, cyanobacterial occurrence along an elevational gradient from

3700 to 5970 m was mainly determined by differences between the studied mountain ranges, but elevation and vegetation type also were relevant (Řeháková *et al.*, 2011). Whereas Oscillatoriales mostly occurred on alpine meadows, Nostocales were dominant in the subnival zone and screes (Řeháková *et al.*, 2011).

Besides photoautotrophic partners close to the soil surface, biocrusts comprise a variety of heterotrophic bacteria, archaea, and fungi (Maier *et al.*, 2018). Whereas the heterotrophic bacterial communities within biocrusts appear to be impacted by the dominating photoautotrophs (i.e. cyanobacteria, algae, lichens, or bryophytes), for microfungi such a link was not observed (Maier *et al.*, 2018). Along an aridity gradient on the Tibetan Plateau, algae-dominated biocrusts hosted more diverse bacterial communities, with diversity increasing with greater aridity, while in lichen-dominated biocrusts bacterial communities were less diverse and bacterial diversity decreased with higher aridity. Besides aridity, bacterial communities were also influenced by environmental and stochastic processes, with the latter governing spatial variations in lichen-dominated biocrusts (Wei *et al.*, 2022a). In alpine biocrusts, the soil–lichen interface was colonised by characteristic bacteria, namely Alphaproteobacteriota and Acidobacteriota (Muggia *et al.*, 2013). Thawing of permafrost and glaciers produces particularly suitable habitats for biocrusts. Accordingly, apart from long-established cryptogam communities, (cyano-)bacteria, (lichenised) fungi, and algae play a key role in primary substrate colonisation after glacier retreat. This has been investigated in different alpine regions around the world, including Norway, Chile, Peru, and in the European Alps (Frey *et al.*, 2013; Bilovitz *et al.*, 2014b; Matthews & Vater, 2015; Krisai-Greilhuber *et al.*, 2017). In Tierra del Fuego, Chile (Cordillera Darwin, Patagonian Andes), bacterial communities with cyanobacteria and algae of the order Prasiolales were the dominant groups close to the glacier terminus, whereas lichen-forming and parasitic fungi occurred in early successional stages (Fernández-Martínez *et al.*, 2017). Cyanobacteria hosted by bryophytes and fertilising the immature soils by actively fixing atmospheric nitrogen were also observed 4–7 years after deglaciation (Arróniz-Crespo *et al.*, 2014). Cyanobacteria were further described to play a vital role in primary succession with respect to both carbon and nitrogen fixation and soil stabilisation at high elevations (5000 m) in the Cordillera de Vilcanota (Cordillera Oriental, Peru) (Schmidt *et al.*, 2008). In the case of lichens, multiple studies in the European Alps describe an increasing abundance and diversity with moraine age (e.g. Bilovitz *et al.*, 2014a,b, 2015) and higher coverage compared to the surrounding non-glaciated area (Hestmark, Skogesal & Skullerud, 2007). In central Svalbard (i.e. arctic climate), repeated surveys of glacier forefields 10–20, 30–50, and 80–100 years after glaciation detected a marked shift in cryptogam community structure over time (Pessi *et al.*, 2019).

An additional effect of biocrusts is their influence on soil temperature. This was shown for instance on the Tibetan Plateau, where Ming *et al.* (2022) found that biocrusts reduced soil temperature by 0.6–1.0°C at a depth of 5–100 cm; Xu *et al.* (2020a) showed similar effects for moss-dominated biocrusts. These results differ from previous studies, where biocrusts increased surface temperatures due to their dark colour (Chamizo *et al.*, 2013). A possible explanation is the high insulating potential of soil organic matter and the high water-holding capacity of the local biocrusts (Ming *et al.*, 2022). Biocrusts on the Tibetan Plateau (i.e. Min Mountains and Qilian Mountains), were also observed significantly to reduce soil pH in the upper 10 cm (Xu *et al.*, 2020a) and to impact seed germination, thus influencing vascular plant community composition (Li *et al.*, 2016b). In another study, biocrusts tended to support the survival of *Nothofagus pumilio* (Poepp. & Endl.) Krasser tree seedlings in the southern Patagonian Andes (Pissolito, Garibotti & Villalba, 2021).

Land use by agriculture and recreational activities can severely threaten biocrusts. For example, in high-elevation grasslands of the Ötztal Alps (European Alps) in Tyrol, Austria, even weak trampling pressure caused a decrease in the frequency of sensitive species, including fruticose and crustose lichens (Grabherr, 1982). In the Canadian Rockies of Alberta, recreational trails had a substantially lower coverage of lichens and biocrusts as compared to undisturbed sites (Crisfield, Macdonald & Gould, 2012). After disturbance of biocrusts in alpine habitats, restoration could be facilitated by inoculation with mature biocrusts (Letendre, Coxson & Stewart, 2019).

(*d*) *Adaptation strategies*

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

V. SOIL MICROBIOTA

Key messages: soil microorganisms, including archaea, bacteria, fungi, and protists, are essential for mineralisation processes, nutrient cycling, and for plant and animal performance as symbionts. Most soil microorganisms remain inaccessible to culture-based methods, highlighting the need for further advancements in these approaches. Knowledge about the enormous microbial diversity in alpine soils has increased rapidly 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. The understanding of viruses in the soil is still in its early stages. However, viruses are influenced by a range of biotic and abiotic factors, and in turn, they affect all sorts of soil biota and should therefore receive more attention. We found 284 publications dealing primarily and 334 dealing secondarily with alpine microbial soil diversity (i.e. 3 for viruses, 26 for archaea, 328 for bacteria, 248 for fungi, and 13 for protists, excluding broader terms), mainly from the mountain regions of Central Asia (63.3%), Central & Southern Europe (17.5%), and the North American Cordillera (6.3%); see Fig. 6 and Table S6.

(1) Viruses

Viruses are tiny infectious particles that can only replicate within the living cells of a host organism. They consist of genetic material, either DNA or RNA, which may be surrounded by a protein coat and sometimes also a lipid envelope. Viruses are not considered living organisms due to their lack of an independent metabolism; however, they represent the most abundant replicable infectious particles on Earth, occurring in large numbers in many habitats, including soil, and directly and indirectly influence the biota in soils. In the past, the study of viruses relied primarily on electron and epifluorescence microscopy, which allowed the detection of 10^7 to almost 10^{10} virus-like particles (VLPs) per gram dry mass in soils (Williamson *et al.*, 2017). In recent years, with the availability of metagenomic analyses, our understanding has expanded dramatically. Viruses are extremely abundant, highly diverse, and largely uncharacterised (Jansson, 2023). The abundance and diversity of viruses in soils are influenced by a range of biotic and abiotic factors, particularly land use, temperature, pH, and water content (Jansson & Wu, 2023; Coclet *et al.*, 2023). Conversely, viruses also affect soil properties as well as soil biota. The lysis of soil microorganisms or other organisms not only affects the turnover rates and growth dynamics of the hosts but also alters nutrient cycling rates; for example, through the release of carbon and particulate organic matter from lysing cells, known as the viral shunt (Jansson & Wu, 2023).

The importance of viruses in soil has now been recognised, and their abundance, systematics, and impact on the soil ecosystem have been summarised in several recent studies (Han *et al.*, 2017; Hillary *et al.*, 2022; Jansson & Wu, 2023; Carreira *et al.*, 2024). However, studies on RNA viruses are underrepresented due to the greater difficulty in extracting and analysing RNA from soil (Hillary *et al.*, 2022). Important groups of RNA and DNA viruses in soil include Kitrinoviricota, Lenarviricota, and Pisuviricota (at the phylum level for RNA) and Tectiviridae, Myoviridae, and Podoviridae (at the family level for DNA) (Jansson & Wu, 2023). In mountain soils, our literature survey identified only three publications investigating soil viruses and, thus there is extremely limited information globally for soil virus diversity in mountain soils above the treeline (Fig. 6). As improved methodologies allow more extensive investigation of soil viruses, it will become possible to begin to research the diversity, interactions, and roles in alpine systems of the so-called ‘viral dark matter’.

(2) Bacteria and Archaea (prokaryotes)

(a) *Brief introduction of organismal group*

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 their high metabolic diversity (various chemo- and phototrophic ways of life), prokaryotes colonise almost every ecological niche on Earth. Given that the majority (approximately 99%) of soil prokaryotes cannot be cultivated, high-throughput sequencing (HTS) and environmental DNA/environmental RNA (eDNA/eRNA) sampling have become powerful tools for assessing and comparing the diversity of prokaryotes (also for fungi and protists), and assembled metagenomes increasingly help to describe the uncultivable majority (Hug *et al.*, 2016). This has led to new insights into prokaryote and fungal diversity in soils and provided information that was unavailable until about 15 years ago.

(b) *Geographic and taxonomic focus*

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 harbours the largest area of mountain permafrost soils globally (Cheng *et al.*, 2022b). A total of 74.0% of all prokaryote diversity studies in mountain soils were performed in Central Asia (Fig. 6, Table S6). Studies addressing microbial diversity (all prokaryotes, selected studies also including fungi and protists) in mountain permafrost outside of this region were conducted recently in the European Alps (12.7%) (Frey *et al.*, 2016; Luláková *et al.*, 2019; Praeg *et al.*, 2019; Adamczyk, Rüthi & Frey, 2021; Sannino *et al.*, 2021; Fiore-Donno *et al.*, 2024) and high-elevation soils from the Andes, Rocky Mountains, and Alaskan Brooks Range (10.4%) (Lipson & Schmidt, 2004; Nemergut *et al.*, 2005; King *et al.*, 2010; Ricketts *et al.*, 2016; Wagner *et al.*, 2017; Farrer *et al.*, 2019). There are a few notable patterns in the numbers of studies (Fig. 6, Table S6), e.g. in alpine mountain soils in Central Asia bacteria have primarily been studied while in most global regions there is a clear focus on fungal research (Table S6). Whether this is related to a dominant abundance of the studied groups or to the traditions of particular scientific disciplines and methodological aspects cannot be determined. Scientific publications addressing archaeal diversity

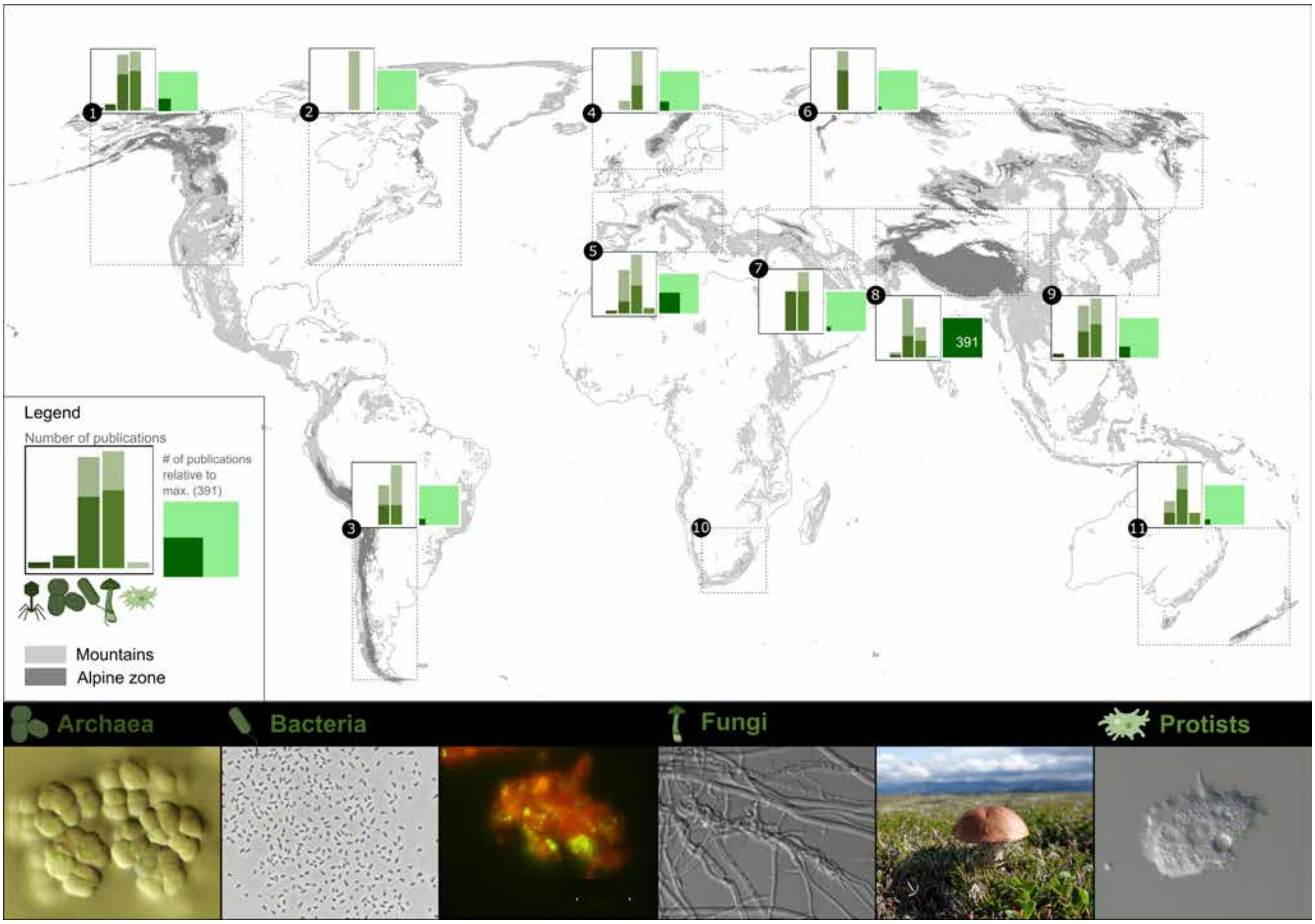


Fig. 6. Global map of the number of publications on microbiota biodiversity in temperate and continental mountain soils above the treeline by alpine mountain region. Number of publications is given per microbial group and relative to the maximum number of publications found (Central Asia, $N = 391$): the dark-coloured part of the bar represents those publications in which this group was deemed the primary focus, the light-coloured part represents those publications where this group was the secondary focus. See Appendix S1 for a detailed description of the methods and Table S6 for publication numbers per region and soil organism group. Icons from Biorender.com. Photographs from left to right: for archaea: *Methanosarcina* sp. (credit: Paul Illmer); for bacteria: *Methylosinus sporium* (credit: Nadine Praeg), DNA (green)-stained soil bacteria attached to soil particle (red) (credit: Nadine Praeg & Paul Illmer); for fungi: *Trichoderma asperellum* Samuels, Lieckf. & Nirenberg intercoiled with *Botrytis* sp. (credit: Siebe Pierson), *Leccinum vulpinum* Watling (credit: Andrea J. Britton); for protists: *Acanthamoeba* sp. (credit: Kenneth Dumack).

specifically are rare, accounting for only 7.3% of the prokaryote literature in mountain soils above the treeline. Of note, studies on soil microbial diversity in mountain regions often analyse prokaryotes and fungi in the same study (Fig. 2B and Table S6). Of all publications with a primary or secondary focus on microbial diversity, 753 publications described microbial diversity only in a non-specific, generic manner (Table S6). This is likely due to methodological constraints, as older methods such as phospholipid fatty acid (PLFA) and Biolog analysis (Xue *et al.*, 2008) provided only broad and imprecise descriptions of microbial communities rather than the more precise analyses of individual taxonomic groups available in the last 20 years. These well-established methods are still in use today; however, as illustrated in Fig. 3, the number of studies has increased significantly with recent advances in molecular high-throughput techniques.

(*c*) *Prokaryote abundances*

Wang *et al.* (2015) reported no clear trend in the abundances of bacteria and archaea across a transect spanning 3106–4479 m on Mount Shegyla (Transhimalaya), Tibetan Plateau; however, they found that the ratio of bacterial to archaeal gene copy numbers (as a proxy for absolute abundances) decreased with increasing elevation, highlighting a switch in favour of archaea. By contrast, Hofmann *et al.* (2016b) did not find a trend in an investigation covering an elevation gradient from 2700 to 3500 m. Liang *et al.* (2023) compared variations in taxonomic and functional (nitrogen cycle) dis/similarity of bacteria across the Tibetan plateau and found both to be driven more by soil abiotic characteristics than by vegetation, but with different environmental drivers prevailing for each. Lazzaro, Hilfiker & Zeyer (2015a) observed the lowest bacterial (and fungal) abundances at the highest site of an elevational transect in the Swiss Uri Alps (1930–2519 m, European Alps). Similar to findings for phylogenetic marker genes, functional gene abundance and diversity were shown to vary with elevation in these studies. Yang *et al.* (2014) studied the functional diversity at four sites along an elevational gradient in the Qilian Mountains (Tibetan Plateau). Abundance of the Rubisco (ribulose-1,5-bisphosphate carboxylase/oxygenase, involved in CO_2-fixation) gene was lower at the lowest site compared to the other sites, which might indicate lower CO_2-fixation activities (Yang *et al.*, 2014; Guo *et al.*, 2015). A succession of the functional genetic potential has also been demonstrated in Swiss glacier forefields (Feng *et al.*, 2023b).

(*d*) *Diversity*

Prokaryote diversity in alpine mountain soils can be comparable to that of sites of lower elevation. Alpine mountain soils harbour considerable bacterial diversity (Rime *et al.*, 2015; Frey *et al.*, 2016) and diversity at high(er) elevations does not necessarily decline like that of plants or animals. Bacteria contribute substantially to biogeochemical cycles, both at the regional and supraregional scale (Donhauser & Frey, 2018) and together with archaea (and fungi, see Section V.3) are considered fundamental in stabilising soils and influencing the physical and biological development of soil ecosystems (Bernasconi *et al.*, 2011). Prokaryote colonisers contribute to the initial build-up of biomass, by fixation of atmospheric CO_2 and N_2 (Frey *et al.*, 2013), and by using carbon and nitrogen from (microbial) necromass (Zumsteg, Schmutz & Frey, 2013b; Rime *et al.*, 2016b; Donhauser *et al.*, 2021). Quantification of precise amounts of CO_2 and N_2 fixation and usage of dead microbial cells as a non-negligible carbon pool in mountain soils is challenging due to the complexity and variability of mountain soils. Further nutrients, such as phosphorus and sulphur, may be obtained from the bedrock by biological weathering (Frey *et al.*, 2010; Brunner *et al.*, 2011). As glaciers increasingly retreat with climate change, barren bedrock is exposed and colonised by pioneer microorganisms such as Acidobacteriota, Planctomycetota, and Bacteroidota (Zumsteg *et al.*, 2012; Rime *et al.*, 2015; Rime, Hartmann & Frey, 2016a). Bacterial candidate phyla OD1, TM7, GN02, and OP11 forming the superphylum Patescibacteria have been recovered from permafrost soils, in addition to well-established phyla such as Proteobacteria (now Pseudomonadota), Verrucomicrobiota, and Acidobacteriota, and were found to represent one-third of the entire community (Frey *et al.*, 2016). At lower elevations, e.g. in alpine grasslands, bacterial communities are primarily dominated by Acidobacteriota [subgroup 6 (and Vicinamibacteria), Acidobacteria], Actinobacteriota (Actinobacteria, Thermoleophilia), Proteobacteria (Alpha- and Gammaproteobacteria), Bacteroidota (Bacteroidia), and Verrucomicrobiota (Yuan *et al.*, 2014, 2015; Yashiro *et al.*, 2016; Chen *et al.*, 2020a, 2021a; Ji *et al.*, 2020; Rui *et al.*, 2023; Fiore-Donno *et al.*, 2024), consistent with the global dominance of Actinobacteriota, Acidobacteriota, and Proteobacteria in global soil studies (e.g. Delgado-Baquerizo *et al.*, 2018); however, Betaproteobacteria are less prominent in alpine soils compared to their global prevalence. Gemmatimonadota and Bacillota (formerly Firmicutes) are also common in alpine grasslands, such as in the European Alps and the Tibetan Plateau (Broadbent *et al.*, 2021; Jiang *et al.*, 2021d), and recently, a higher prevalence of Myxococcota in alpine soils was described (Fiore-Donno *et al.*, 2024). Studies specifically addressing archaeal communities in alpine grasslands are rarer (Fig. 6, Table S6). However, existing work suggests that Thaumarchaeota (Nitrososphaeria), Nanoarchaeota, Woesearchaeota, Crenarchaeota (Bathyarchaeota, Thermoprotei), and Euryarchaeota (Thermoplasmata, Methanobacteria) are the most prevalent archaeal phyla (Malard *et al.*, 2022; Fiore-Donno *et al.*, 2024). Ongoing changes in microbial taxonomy, for archaea (and bacteria), facilitated by the increasingly widespread availability of genome sequences and the development of comprehensive sequence-based taxonomies like the Genome Taxonomy Database (GTDB) (Parks *et al.*, 2018) will also need to be considered. The coverage of archaea can be less than 25% when using universal primers for 16S rRNA gene metabarcoding (Bahram *et al.*, 2019) and selective and specific detection of archaea has rarely been carried out and is urgently needed. The dominance of Actinobacteriota and Acidobacteriota and especially of ammonium-oxidising archaea within the prokaryote community is likely due to their adaptation to the nitrogen- and phosphorus-limited conditions typical of alpine grassland soils or higher elevation soils (Liu *et al.*, 2017; Ma *et al.*, 2019c; Praeg *et al.*, 2019).

(*e*) *Drivers*

In alpine systems, the composition, distribution, and structure of microbial communities depend on a number of environmental factors. In line with global studies (e.g. Delgado-Baquerizo *et al.*, 2018) not focusing on or including alpine soils, research on alpine environments has shown that temperature, precipitation, and soil pH are key drivers of bacterial community composition. Other climatic variables such as moisture and snow cover duration (Malard *et al.*, 2022), substrate and nutrient availability (e.g. Shen *et al.*, 2015a), biotic interactions (Fiore-Donno *et al.*, 2024), slope aspect (Adamczyk *et al.*, 2019), as well as other soil physicochemical and vegetation properties (Donhauser & Frey, 2018; Adamczyk *et al.*, 2019; Praeg *et al.*, 2019, 2020; Liang *et al.*, 2023) have been shown to impact bacterial community structure. While temperature and precipitation typically have a direct effect on microbial communities, the effects of soil, the rhizosphere and plant-derived organic matter can be indirect and depend on climatic variables as well as biological and chemical feedback. Yet, the establishment of plants has been identified as an important driver of prokaryote community structure during early succession (Rime *et al*., 2015; Wojcik *et al*., 2020). Overall, edaphic factors such as soil pH, organic matter content, water, and available phosphorus concentrations (Yashiro *et al*., 2016; Bueno de Mesquita *et al*., 2020b) remain the main determinants of bacterial and archaeal richness, diversity, and community composition. Soil transplantation experiments to investigate changes in the taxonomic and functional gene composition of microbial communities with warming (Zumsteg *et al*., 2013a; Rui *et al*., 2015) have confirmed field observations. In these studies, changes in community structure were attributed to temperature, moisture, soil properties, and vegetation parameters. By condensing information on community composition to microbial richness and diversity indices, it was shown that bacterial richness decreased with increasing elevation (Shen *et al*., 2015a; Adamczyk *et al*., 2019; Praeg *et al*., 2019), whereas for archaea, Singh, Takahashi & Adams (2012a) documented a peak in alpha-diversity at mid-elevations along a 1000–3760 m gradient on Mount Fuji (Kantō Mountains), Japan. In glacier forefield soils, microbial community composition was reported to shift in response to increasing carbon content in soils, decreasing soil pH, and plant establishment (Zumsteg *et al*., 2012). Ficetola *et al*. (2024) conducted a comprehensive analysis of 46 proglacial landscapes worldwide, assessing soil properties, microclimate, productivity, and biodiversity through eDNA metabarcoding. Their findings show that environmental properties evolve as glaciers retreat, with temperature influencing soil nutrient accumulation. Bacterial (and fungal) richness increased over time since deglaciation, as microorganisms begin colonising within the first few decades. Additionally, plant communities in glacier forefields interact positively with soil animals and microorganisms, and were shown to play a crucial role in ecosystem development.

Temperature further affects microbial communities when it reaches extremes (>25°C) and passes a tipping point where microorganisms react to further temperature increase with pronounced non-linear responses in community-level growth rates, changes in the temperature sensitivity of bacterial growth (Q_{10}), and alterations in community structure (Donhauser *et al*., 2020, 2021). While fungal communities are tightly associated with plants (see Section V.3), bacterial and archaeal communities are also influenced by the diversity of the respective other prokaryote group (Malard *et al*., 2022).

As detailed in Section III.1, climate (including snowpack depth, duration and snowmelt) and soil properties are seasonally variable (Shen, He & Ge, 2021), with seasonality itself being increasingly influenced by climate change (Ernakovich *et al*., 2014). The transition from winter to summer was most pronounced for Acidobacteriales, with snowmelt specifically triggering an abrupt shift in the composition of soil prokaryotes (Broadbent *et al*., 2024). Reduced snow cover, which is expected under climate change in some mountain regions (Notarnicola, 2022), might advance this seasonal transition. Short-term seasonal changes (e.g. within the summer season from June to September) showed pronounced effects on the prokaryote community structure driven by aboveground biomass, precipitation, and soil temperature (Rui *et al*., 2023) and with Actinobacteriota being particularly sensitive to short-term changes such as monthly fluctuations in precipitation. These results indicate that elevation, sampling season, and their interaction accounted for 19%, 22%, and 12% of the prokaryote community variation, respectively (Rui *et al*., 2023). Lazzaro *et al*. (2015a) showed that, under winter snowpack, bacterial communities were dominated by Betaproteobacteria, while in the snow-free seasons other groups (i.e. Cyanobacteria) became more abundant, thereby confirming that bacterial community structures exhibit pronounced annual cycles.

Soil functions and processes are driven by microbial interactions, and the study of co-occurrence networks among bacterial, archaeal, and fungal microbiota is gaining interest, although the inference of interactions using correlation-based data is limited. So far, in alpine grasslands, soil pH was found to be a key driver for predicting network-level topological features of soil microbial co-occurrence networks; with increasing soil pH, associations between microorganisms were enhanced and networks became more stable (Chen *et al*., 2021a). Traditional compartmentalised views on soil microbial diversity should be challenged, emphasising ecosystem interconnectedness of microorganisms (archaea, bacteria, fungi) among soil organisms (e.g. invertebrates). Underscoring the need for a holistic understanding of prokaryote diversity in soil, Galla *et al*. (2023a,b) provided experimental procedures intended to reduce methodological variability essential for ecosystem-level soil microbiodiversity studies.

Overall, central gaps in knowledge about prokaryote diversity in alpine soil still exist, particularly in a geographical context. From Fig. 6 it is obvious that the global distribution of microbial studies is not uniform and displays distinct disparities in the level of research activity in various areas. Secondly, there remains a lack of knowledge about the activity and ecological functions of prokaryotes *in situ*. While molecular data provide information about phylogeny, conclusions about the functions of specific clades are often drawn from a few cultured isolates, which may not be representative for the entire group (e.g. Verrucomicrobiota).

(3) Fungi

(*a*) *Brief introduction of organismal group*

Fungi comprise a large ecologically heterogenous group of microorganisms (Stajich *et al*., 2009), of which only 2–6% of the estimated 1.5–12 million species have been formally described (Taylor *et al*., 2014; Hawksworth & Lücking, 2017; Bhunjun *et al*., 2022). Functionally, fungi range from key players in (re-)cycling of carbon, nitrogen, and other elements in terrestrial ecosystems, as the main saprotrophic decomposers of (recalcitrant) organic materials (Baldrian & Valásková, 2008; Finlay & Thorn, 2019), to those forming a great diversity of symbiotic associations with plants and animals (Mueller & Gerardo, 2002; Crowther, Boddy & Hefin Jones, 2012; Genre *et al*., 2020). Until almost two decades ago, much of what is known concerning alpine soil fungal communities came from European and North American studies of the macroscopic reproductive structures (the sporocarps) produced by fungi. Studies include taxonomic works (Horak, 1993; Cripps, Larsson & Horak, 2010), community and biogeographic studies (Senn-Irlet, 1988, 1993; Ronikier, 2008), and ecological investigations (Graf, 1994). These studies have identified a rich diversity of saprotrophic and plant-associated symbionts, many of which appear to be restricted to alpine and arctic environments (Cripps *et al*., 2019). For the last 15 years, a rapidly increasing number of metabarcoding studies have included analyses of whole fungal communities in alpine soils (Fig. 3).

(*b*) *Geographic and taxonomic focus*

A majority (72.5%) of fungal diversity studies in mountain soils are from the alpine mountain regions of Central Asia and Central & Southern Europe (Fig. 6, Table S6). In addition, there is a clear focus on fungal research in northern regions (North American Cordillera, Appalachians & Northeast Ranges, Northern Europe, Northern Asia) but also in Australia and New Zealand (Fig. 6). Note also from Table S6 that 753 publications only referred to microbial diversity in a non-specific, generic manner, indicating that assigning them to specific microbial groups such as fungi was not feasible.

(*c*) *Diversity*

In alpine grasslands, soil fungal communities contain considerable proportions of unidentified fungi but are primarily composed of Ascomycota and Basidiomycota (Pellissier *et al*., 2014; Malard & Pearce, 2018; Praeg *et al*., 2020). Within these phyla, Agaricomycetes (Basidiomycota), Archaeorhizomycetes (Ascomycota), Sordariomycetes (Ascomycota), and Leotiomycetes (Ascomycota) are the most abundant classes of fungi in grasslands (Pellissier *et al*., 2014; Pinto-Figueroa *et al*., 2019), highlighting the dominance of Ascomycota within fungal communities. This observation is consistent with findings in global soil fungal communities, although alpine soils are less frequently or not included in such studies (e.g. Egidi *et al*., 2019; Větrovský *et al*., 2019). Agaricomycetes are commonly saprotrophic (decomposers) and actively participate in the decomposition of organic matter (Ludley & Robinson, 2008; Edwards & Zak, 2010), especially in cold and dry environments (Ludley & Robinson, 2008). Sordariomycetes and Leotiomycetes are ecologically diverse and include pathogens of either plants or animals, mycorrhiza and plant endophytes, as well as saprotrophs (Maharachchikumbura *et al*., 2016; Johnston *et al*., 2019). Finally, the Archaeorhizomycetes are a widely distributed and abundant class of terrestrial fungi, yet their ecosystem roles are still debated (Rosling, Timling & Taylor, 2013; Pinto-Figueroa *et al*., 2019). While thought to be linked with plant roots, experiments have indicated that they are neither mycorrhizal nor pathogenic (Rosling *et al*., 2013). Additionally, their (semi-quantitative) detection in metabarcoding studies varies when using the ITS2 region or the 18S rRNA gene, which can be explained by primer biases (Rosling *et al*., 2013; Tonjer *et al*., 2021). In the European Alps, fungi are locally diverse (Brunner *et al*., 2017; Adamczyk *et al*., 2019; Praeg *et al*., 2019; Arraiano-Castilho *et al*., 2021), similar to other alpine regions (Bjorbækmo *et al*., 2010; Perez-Mon, Frey & Frossard, 2020; Rüthi *et al*., 2020).

In mountain regions, glacier forefields have been the focus of intensive studies on fungal community composition, revealing that the active fungal community shifts in response to different soil developmental stages (Zumsteg *et al*., 2012, 2013b; Rime *et al*., 2015; Sannino *et al*., 2020). After glacier retreat, fungi immediately (<10 years) develop rich communities, reaching a plateau after around a century. This may coincide with the peak of diversity in some microorganism groups 50–100 years after the initiation of soil development, followed by the replacement of pioneer oligotrophic taxa with copiotrophic taxa (organisms adapted to environments poor or rich in nutrients, respectively) or by microorganisms associated with early-coloniser plants being replaced by those linked to late succession as vegetation shifts from open habitats to closed forests (Ficetola *et al*., 2024). In detail, the diversity of fungi was high in barren ground closest to the glacier tongue and was similar to older vegetated soils (Rime *et al*., 2015; Dresch *et al*., 2019). Glacier ice is considered as a fungal (and prokaryote) inoculum source for the earliest ice-related barren ground and for later plant-covered soil (e.g. by wind-born propagules, spores, melt water) (Rime *et al*., 2016a). Besides the glacier environment, permafrost soils also accommodate numerous ancient fungi (Frey *et al*., 2016; Luláková *et al*., 2019; Pontes *et al*., 2020; Frey, 2021). European permafrost soils are dominated by lichenised fungi and basidiomycetous *Rhodotorula*, including the genera *Naganishia*, *Mrakia*, and *Leucosporidium* (Frey *et al*., 2016; Adamczyk *et al*., 2021; Sannino *et al*., 2021).

(*d*) *Interactions*

Historically, below-ground studies of alpine fungi have focused on ectomycorrhizal (ECM, sometimes abbreviated as EM) and arbuscular mycorrhizal (AM) fungi as well as root-associated symbionts of plants. However, there are very few studies on fungal symbionts associated with ericaceous plants (ericoid mycorrhizal fungi), despite the importance of heath vegetation in alpine systems (Kivlin *et al*., 2017). ECM fungi are nevertheless essential for establishment and habitat colonisation by alpine plants such as willows (Nara & Hogetsu, 2004). Ectomycorrhizal fungal communities have been examined on a range of hosts, using combinations of linking sporocarps to associated ECM tips (*Salix herbacea* L.; Graf & Brunner, 1996) or selection of ECM tips followed by molecular identification [*Dryas* sp. and *Salix* sp. (Kernaghan & Harper, 2001); *Arctostaphylos uva-ursi* (L.)

Spreng. (Krpata *et al.*, 2007); *Bistorta vivipara* (L.) Delarbre (Thoen *et al.*, 2019)]. Gao & Yang (2016) used a cloning approach to examine mycorrhizal fungi on herbaceous plant roots in alpine meadows in southwestern China (Hengduan Shan). However, metabarcoding studies have provided more comprehensive assessments of root-associated fungi on particular host species, including *Arctostaphylos* sp. (Hesling & Taylor, 2013), *Dryas* sp. (Bjorbækmo *et al.*, 2010), *Carex myosuroides* Vill. (Mühlmann & Peintner, 2008), *Bistorta vivipara* (Mühlmann, Bacher & Peintner, 2008), and *Salix* spp. (Ryberg, Andreasen & Björk, 2011). A recent barcoding study by Arraiano-Castilho *et al.* (2021) demonstrated that habitat was a stronger determinant than the host plant for ECM fungal distribution in alpine habitats.

Fungi carry out a multitude of functions in ecosystems, and although they interact with many trophic groups, the major focus has so far been on plant-associated symbionts. The importance of fungal–plant interactions in the development of plant communities has been particularly well investigated at glacial fronts in alpine zones using metabarcoding studies in Norway (Southern Scandes; Blaalid *et al.*, 2012), Switzerland [Uri Alps (Brunner *et al.*, 2011; Rime *et al.*, 2015)], and the USA (Cascade Mountains; Jumpponen *et al.*, 2015).

(*e*) *Drivers*

Besides biotic (plant) influences, fungal communities in alpine grasslands are primarily affected by edaphic and climatic parameters. Specifically, soil pH, soil organic carbon, nitrogen, soil water content, and electrical conductivity are important soil variables, with snow cover duration also exerting a significant influence on fungal richness (Pellissier *et al.*, 2014; Yang *et al.*, 2017b; Malard *et al.*, 2022). This is not consistent with global (meta-)studies on soil fungal communities which showed that soil properties were poor predictors of the dominant fungal taxa (Tedersoo *et al.*, 2014; Egidi *et al.*, 2019). Global studies rarely include alpine soils; however, global and alpine soil fungal studies agree on the importance of climate parameters (e.g. temperature, precipitation) in determining fungal richness, composition and community assembly dynamics (Tedersoo *et al.*, 2014; Bahram *et al.*, 2018; Větrovský *et al.*, 2019). The importance of microtopography in alpine zones, particularly differences in snow cover (duration), 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) are likely to 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. While global studies on soil fungi suggest that plant diversity does not broadly affect fungal diversity, this general trend does not apply to ectomycorrhizal fungi (Tedersoo *et al.*, 2014). By contrast, plant richness and diversity are key to fungal alpha and beta diversity in alpine grasslands (Pellissier *et al.*, 2014; Yang *et al.*, 2017b; Malard *et al.*, 2022). Another factor, 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). Additionally, elevated nitrogen deposition induces major shifts in soil fungal functional groups (van der Linde *et al.*, 2018; Zhang, Chen & Ruan, 2018c) which agrees with the findings of global studies (Mikryukov *et al.*, 2023). Fungal community studies in alpine grassland, e.g. in China (Yang *et al.*, 2018) and Central Europe (e.g. Pellissier *et al.*, 2014; Praeg *et al.*, 2019), demonstrated that different functional groups show a range of responses to changes in elevation, temperature, nitrogen addition, and grazing management. Compared to other functional groups, the effect of environmental properties on pathogenic fungal diversity is weaker on a global scale; however, Mikryukov *et al.* (2023) demonstrated that in alpine habitats where diurnal temperature amplitudes fall outside the range of 7–13°C, pathogenic fungal diversity declines.

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).

(4) Protists

(*a*) *Brief introduction of organismal group*

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). For example, protist taxa cover size ranges from a few micrometres (comparable to sizes of yeasts and larger bacteria) to those that can grow to several centimetres, such as slime moulds (Geisen *et al.*, 2017). In soils, protists feed on a wide variety of substrates, with heterotrophs representing the most abundant and diverse functional group (Bonkowski, Dumack & Fiore-Donno, 2019). Soil protists were first shown to be key bacterial predators that control bacterial abundances and, *via* the microbial loop, make nutrients available for plant growth (Clarholm, 1985). However, protist predators occupy different trophic niches, feeding on a range of microorganisms including bacteria, fungi, algae, as well as micro-metazoa such as nematodes and rotifers (Yeates & Foissner, 1995; Gilbert *et al.*, 2000; Jassey *et al.*, 2013; Geisen *et al.*, 2015; Estermann *et al.*, 2023), and also other protists (Seppey *et al.*, 2017; Geisen *et al.*, 2018; Bonkowski *et al.*, 2019). In these cases, phagocytosis appears to be the main mechanism for nutrient acquisition (Singer *et al.*, 2021). While soil protists have long been neglected in soil microbiological studies (Geisen *et al.*, 2020), they now are the focus of an increasing number of studies as their importance as determinants of plant performance has become established (Bonkowski, 2004; Gao *et al.*, 2019). Thus, protists are now recognised as important elements in soil ecosystems due to their role in the microbial food web and nutrient cycling (Adl & Gupta, 2006; Geisen *et al.*, 2016) and their contribution to biogeochemical cycles, especially carbon (Geisen *et al.*, 2020) and silicon (Aoki, Hoshino & Matsubara, 2007).

(*b*) *Geographic and taxonomic focus*

Only a few studies have attempted to characterise protist communities in alpine ecosystems (Hu *et al.*, 2022c; Kang *et al.*, 2022) and those are geographically concentrated in Central & Southern Europe and Central Asia (Fig. 6, Table S6). Due to the methodological challenges associated with the study of soil microorganisms, many of which cannot be grown easily in the laboratory, the diversity of protists living in oceans and freshwater ecosystems is better documented than that of soil protists. However, high-throughput sequencing studies are revealing that their diversity is highest in soils, partly due to the strong heterogeneity of the soil environment and diversity of soil types (Singer *et al.*, 2021). Thus, while some studies have explored the diversity of individual protist groups in mountain soils, documentation of this diversity beyond high-throughput sequencing approaches still represents a largely open field of research, as is true for microscopic soil organisms in general (Decaëns, 2010).

(*c*) *Diversity*

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 *et al.*, 2019). Although some protist taxa, such as the family Grossglockneriidae (Petz *et al.*, 1986), were described in the European Alps, and Santibáñez *et al.* (2011) discovered *Puytoracia jenswendti* SANTIBÁÑEZ *ET AL.*, 2011, a euglyphid testate amoeba, on glaciers in the Patagonian Andes, the degree of endemicity among alpine protist taxa remains to be determined (Ronikier & Ronikier, 2009). Recent decades have revolutionised our perspective on soil protist functional roles, which span the whole spectrum from primary producers, photo- and saprotrophs, decomposers, and predators, to parasites (Geisen *et al.*, 2018, 2020). Stramenopiles, Alveolates, and Rhizaria (SAR), along with Amoebozoa and Archaeplastida dominate protist diversity in alpine grasslands (Seppey *et al.*, 2020). Diversity patterns of soil protists along elevation gradients have primarily been investigated for specific groups, such as testate amoebae. Testate amoebae, the term used for a polyphyletic group of shelled protists, are commonly used as models for biogeographic studies. Along such elevation gradients, contrasting patterns of distribution were observed: a hump-shaped pattern along the gradient (e.g. Krashevska *et al.*, 2007; Krashevska, Maraun & Scheu, 2010; Lamentowicz *et al.*, 2013), the lowest diversity at mid-elevations (Tsyganov *et al.*, 2022), decreasing richness, diversity, and evenness with increasing elevation (Heger *et al.*, 2016), or no response to elevation (Mitchell, Bragazza & Gerdol, 2004; Shen *et al.*, 2014). These contradictory patterns reflect the high diversity of protists, but also likely the fact that some groups are poorly recovered, either due to the fact that primers are not totally universal (e.g. Amoebozoa are typically underestimated) or that the barcode used (e.g. V4 region of the 18S rRNA gene) contains insertions (e.g. in some common soil Rhizaria) that make it impossible to use short reads, as in Illumina sequencing (Pawlowski *et al.*, 2012). In terms of functional diversity, consumers (i.e. feeding on other living individuals) are numerically the most abundant group in the soil, followed by parasites and phototrophs (Mazel *et al.*, 2022). The dominance of consumers in soils of montane ecosystems suggests that this functional group could be key in the cycling and turnover of nutrients in this type of ecosystem (Geisen *et al.*, 2018; Oliverio *et al.*, 2020).

(*d*) *Drivers*

Due to the large variation in traits among protist species, distinct species do not necessarily respond uniformly to environmental gradients. Nonetheless, as in other habitats, the majority of protistan taxa in alpine soils are believed to be small, motile, and cyst-forming bacterivores (Oliverio *et al.*, 2020; Kang *et al.*, 2022). Accordingly, only a small effect of elevation on alpha and beta diversities of protistan communities is expected.

As is known from low-elevation soils, edaphic factors (e.g. soil moisture, carbon content, and soil pH) and the local plant community are strong determining factors of soil protist communities (Shen *et al.*, 2014; Oliverio *et al.*, 2020; Aslani *et al.*, 2022). Besides edaphic factors, temperature and slope of mountain systems also drive protist community assemblages (Seppey *et al.*, 2020; Malard *et al.*, 2022). Likewise, Hu *et al.* (2022c) showed a strong influence of soil moisture and nitrogen content as shaping factors of soil protistan communities at high elevations, while Shen *et al.* (2014) found protist communities to be primarily correlated with soil pH. Body size is relevant for dispersal and tolerance to stress as smaller species are more easily transported (Wilkinson *et al.*, 2012) and respond better to stressors like drought (Marcisz *et al.*, 2020). Thus, body size can be considered a response trait, with stressors like drought and frost acting as ecological filters that shape community composition. Consequently, deterministic factors (e.g. soil acidity, temperature) are considered more important in the assembly of protist communities than for other microbes (Hu *et al.*, 2022c; Kang *et al.*, 2022). Furthermore, Kang *et al.* (2022) showed that turnover rates among alpine environments were lower for protists than for other microorganisms (bacteria and fungi), which they argued was due to a higher dispersal rate of motile protists. Borg Dahl *et al.* (2019) highlighted the importance of plant community as a major determinant for the community composition of Myxomycetes in the European Alps. Physicochemical properties and vegetation patterns, thus, differentially shape protists in mountain forests, shrublands, grasslands, pastures, and high alpine zones. To test these trends and hypotheses on protist communities, more targeted inventories are needed across alpine systems. A recent study manipulated precipitation, warming, and nitrogen addition in alpine habitats, revealing that these global change factors fundamentally altered soil protist communities and their abundances. In this study, increased precipitation and nitrogen input caused an increase in protist diversity and abundance, respectively, while decreased precipitation and warming reduced them (Hu *et al.*, 2022c). It can be expected that changes in bacterial, fungal, and also plant and animal communities will have cascading effects on protists (Valencia *et al.*, 2018). Climate change is expected to alter protist communities in alpine habitats with potential impacts on other components of the soil microbiome and on soil functions (Mazel *et al.*, 2022).

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

Soil protists, including crop pathogens like *Phytophthora infestans* (MONT.) DE BARY, have a broader role as parasites, potentially affecting plants or soil animals. However, the diversity and interactions of these protist parasites remain understudied. A study in the Swiss Alps showed that the diversity of Apicomplexa, parasites of invertebrates and vertebrates, in various alpine habitats correlated positively with the diversity of their putative metazoan hosts (Singer *et al.*, 2020). The relative contribution of parasites to the total protist community compared to other functional groups was, however, shown to decrease with increasing elevation, likely due to a reduction in host density with elevation (Mazel *et al.*, 2022).

Phototrophic protists, like *Chlorella* and *Trebouxia*, are common as symbionts in lichens, but also as free-living forms at the soil surface (Jassey *et al.*, 2022). However, the abundance of free-living phototrophic protists (and their predators) is highest in moist (e.g. peatlands) and open (e.g. arid or alpine) vegetation (Gilbert *et al.*, 1998; Seppey *et al.*, 2017). In arid habitats, including patchy alpine vegetation, phototrophic protists contribute to the formation of biocrusts, which are major contributors to organic carbon and nitrogen fixation (Dickson, 2000) and reduce soil erosion (Evans & Johansen, 1999). Although there is a growing number of studies in mountain systems, there is a need for deeper insights, particularly because our understanding of alpine protists lags behind that of arguably most other groups of soil organisms.

VI. SOIL FAUNA

Key messages: the treeline ecotone harbours a high diversity of soil micro-, meso-, and macrofauna, as species from both forest and grassland ecosystems coexist. At higher elevation, the shallow soils are mainly inhabited by soil meso- and microfauna. 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 zone is mainly carried out by Nematocera larvae and Collembola). Food webs in high alpine soils are simple, with fewer interactions compared to soils at lower elevations. Omnivorous and opportunistic feeding habits increase to ensure energy intake. Extensive grazing by livestock and wild mammals can improve conditions for decomposers within the soil fauna by providing nutritious dung and reducing cover of dwarf shrubs and their recalcitrant litter. We found 148 publications dealing primarily and 25 dealing secondarily with alpine soil fauna (i.e. excluding studies with a generic focus: 46 for both micro-, and mesofauna, 81 for macrofauna), mainly from the mountain regions of Central & Southern Europe (41.6%), Central Asia (24.9%), and Northern Europe (9.2%); see Fig. 7 and Table S7.

(1) Brief introduction of organismal group

Alpine soil fauna comprises a wide range of taxa and includes all major invertebrate groups that also inhabit soils at lower elevations. Their diversity is particularly high close to the treeline, where representatives of all size classes of soil fauna – microfauna (mainly nematodes, rotifers, and tardigrades), mesofauna (mainly collembolans, mites, and enchytraeids), and macrofauna (mainly earthworms, spiders, myriapods, isopods, ants, and insect larvae) – are found (Orgiazzi *et al.*, 2016), and where grassland species co-occur with forest species, especially in intertwined dwarf shrub habitats. Above the treeline, many soil macrofauna taxa decrease in numbers with increasing elevation due to climatic and

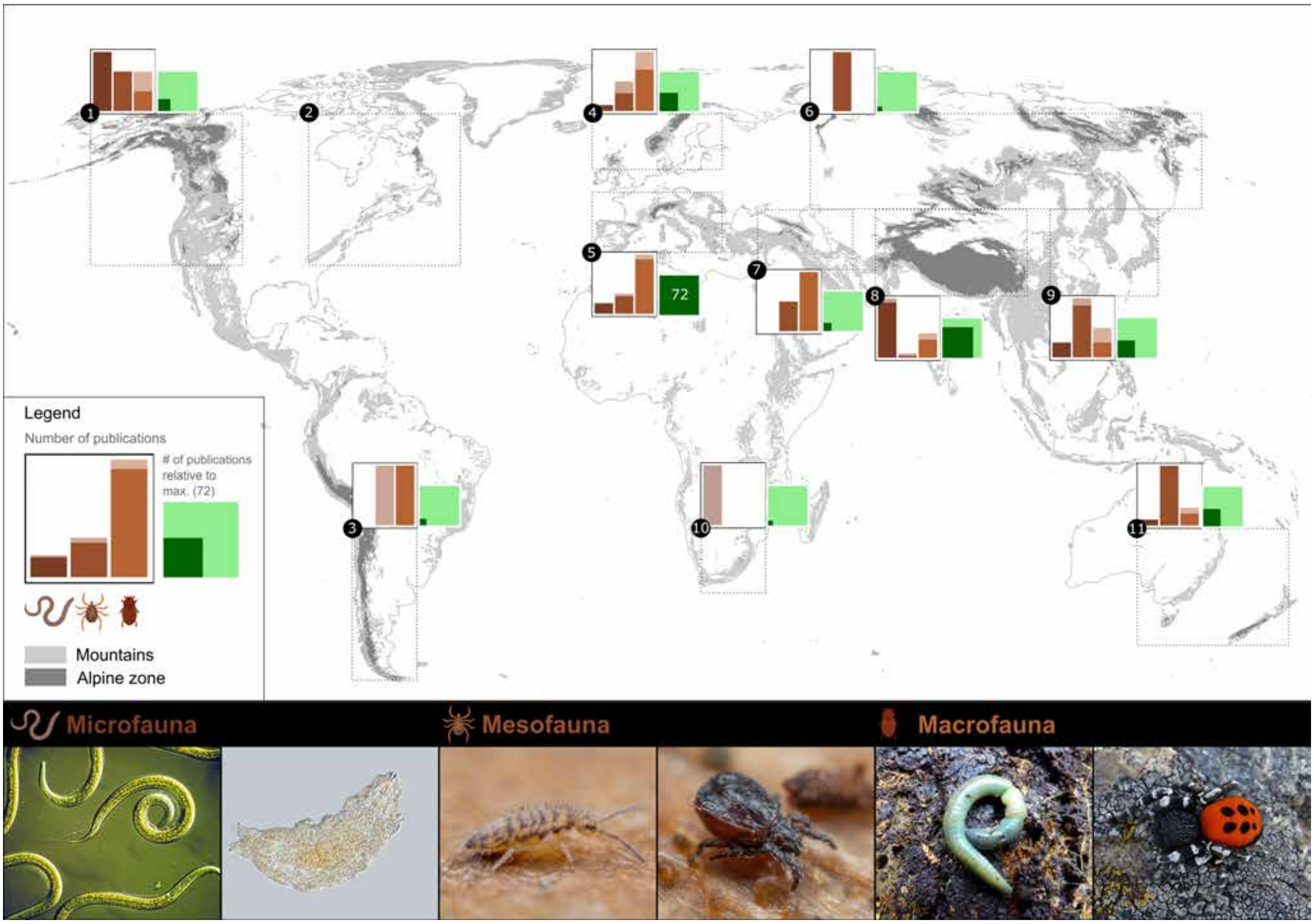


Fig. 7. Global map of the number of publications on fauna biodiversity in temperate and continental mountain soils above the treeline by alpine mountain region. Number of publications is given per faunal group and relative to the maximum number of publications found (Central & Southern Europe, $N = 72$): the dark-coloured part of the bar represents those publications in which this group was deemed the primary focus, the light-coloured part represents those publications where this group was the secondary focus. See Appendix S1 for a detailed description of the methods and Table S7 for publication numbers per region and soil organismal group. Icons are taken from Biorender.com. Photographs from left to right: for microfauna: microscope images of nematodes (credit: CSIRO Entomology), and the tardigrade *Macrobiotus* sp. (credit: Michala Tůmová); for mesofauna: the springtail *Entomobrya nivalis* (C. Linnaeus, 1758) and the mite *Platynothrus pelitfer* (Koch, 1989) (credits: Frank Ashwood); for macrofauna: the 'green' earthworm *Aporrectodea smaragdina* (Rosa, 1892), which inhabits calcareous mountain soils in the European Alps and Dinaric Alps, and the male velvet spider *Eresus sandaliatus* (Martini & Goeze, 1778) found in alpine dry pastures in the Central European Alps (credits: Michael Steinwandter).

topographic conditions. Vegetation cover and soil depth decrease steadily with elevation, limiting soil macrofauna that require litter-producing plants and/or the physical habitat space provided by soils in general. Nonetheless, representatives of the soil meso- and microfauna can still be abundant in shallow high-elevation soils.

In alpine environments, soil fauna is generally sampled by installing pitfall traps (macrofauna, partially also mesofauna), by taking soil core samples (all groups), by suction sampling (ground-dwelling mesofauna), as well as *via* hand sorting and hand searching (meso- and macrofauna). At higher elevations, pitfall traps are often preferable over soil core samples as soil becomes increasingly shallow, but hand searching may be more efficient for certain specialised taxa (Moret & Gobbi, 2024). To cope with methodological and logistical limitations, additional approaches such as soil biodiversity indices (e.g. QBS-ar, the Soil Biodiversity Quality index using microarthropoda; Maienza *et al.*, 2022) and DNA metabarcoding (e.g. *via* eDNA; Rota *et al.*, 2020) have been increasingly applied in alpine habitats. Amongst the alpine soil fauna species described to date, some exhibit a cryptic lifestyle, making them difficult to detect. However, often records from occasional samplings have led to new discoveries for alpine regions, such as the carabid beetle *Orthoglymma wangapeka* Liebherr, Marris, Emberson & Syrett & Roig-Juñent, 2011 (Liebherr *et al.*, 2011) and the oribatid mite *Crotonia ramsayi* Colloff, 2015 (Colloff, 2015) in New Zealand, the isotomid springtail *Skadisotoma inpericulosa* Greenslade & Fjellberg, 2015 (Greenslade & Fjellberg, 2015) in Australia, and the checkered beetle *Opetiopalpus* *sabulosus* MOTSCHULSKY, 1840 (Steinwandter *et al.*, 2019) in the European Alps.

Even though the number of soil biodiversity studies is growing, data on soil fauna are still scarce and often limited to ground-dwelling taxa (Burton *et al.*, 2022); soil fauna studies focusing on alpine habitats (including nival ecosystems) are especially rare. Available data relate primarily to alpine regions in Central & Southern Europe (Fig. 7, Table S7) such as the European Alps (e.g. Gobbi *et al.*, 2020; Koch & Kaufmann, 2010; Meyer & Thaler, 1995; Puntscher, 1980; Seeber *et al.*, 2021; Chamberlain *et al.*, 2020), Central Asia such as the Tibetan Plateau (e.g. Wu, Zhang & Wang, 2015a; Devetter *et al.*, 2017), and Australia and New Zealand (e.g. Salmon, 1940; Hammer, Foged & Nørvang, 1966; Houston & Greenslade, 1994; Minor *et al.*, 2016; Mesibov, 2018; Green & Slatyer, 2020). By contrast, alpine mountain regions in the Americas (i.e. Rocky Mountains, Appalachians, and Andes), Africa (i.e. Drakensberg), and the Caucasus remain understudied (but see Armstrong & Brand, 2012; Kokhia & Golovatch, 2020); we found only five soil fauna publications for each of these alpine mountain regions (Table S7). Information on alpine soil fauna may be available locally for many alpine regions but published in languages other than English and is therefore not accessible in *Web of Science*.

A high percentage of species is regionally endemic or found in restricted geographical areas, as observed in the European Alps (e.g. 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 expanded extensively (Hill *et al.*, 2009). For Australasian alpine taxa, a deeper phylogeographic structuring was shown compared to European and North American taxa, 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 investigated by observing the (re)colonisation of alpine land when glaciers retreat (Koch & Kaufmann, 2010; Hågvar *et al.*, 2020). The first to (re)colonise the bare land are agile ground-dwelling predators (e.g. carabid beetles, harvestmen, linyphiid and lycosid spiders), which presumably depend on smaller wind-dispersing invertebrates as food sources, along with soil mesofauna (springtails, oribatid mites) and thrips (Thysanoptera). Afterwards, larger detritivores (millipedes, gastropods, woodlice, and dipteran larvae such as Tipulidae, Bibionidae, and Sciaridae) appear when the soil and vegetation are more developed (Kaufmann, Fuchs & Gosterxeier, 2002; Makarova *et al.* 2024).

(2) Soil microfauna

(*a*) *Geographic and taxonomic focus*

Soil microfauna mainly comprises roundworms (Nematoda), rotifers (Rotifera), and water bears (Tardigrada). Relatively little research on these tiny soil invertebrates has been conducted in alpine regions worldwide. We found 46 scientific publications mostly from Central Asia (58.7%), Southern & Central Europe (19.6%), and the North American Cordilleras (6.5%) (Fig. 7, Table S7). The low numbers may partly arise from methodological restrictions, as each soil microfauna taxon needs an appropriate extraction method (Devetter, 2010).

(*b*) *Diversity and drivers of selected microfauna taxa*

Nematodes are by far the most investigated soil microfauna group in alpine soils. A global distribution map of nematodes revealed a positive relationship between organic carbon content in mountain soils and abundance of nematodes (van den Hoogen *et al.*, 2019). Recently, Porazinska *et al.* (2021) showed that soil Nematoda expand their distribution ranges with elevation by following expanding plant species. In studies from European alpine grasslands (High Tatras, Carpathian Mountains; Háněl, 2017) and mountain peaks (Styrian Alps, European Alps; Hoschitz & Kaufmann 2004b), soil Nematoda were found to be abundant, and may be suitable for use as sensitive bioindicators influenced by climatic factors such as freeze–thaw cycles and growing season duration. As plant communities become more complex and diverse, even at higher elevations, due to temperature rise, a more diverse nematode community may increasingly contribute to carbon and nitrogen sequestration. Further, Li *et al.* (2023c) found that soil nematodes – which are generally water-bound – respond positively to higher precipitation and soil water content in alpine grasslands of the Tibetan Plateau, with higher-trophic-level nematodes (i.e. omnivores, carnivores) showing stronger effects than lower-trophic-level nematodes (i.e. bacterivores, fungivores). Generally, it was found that different functional groups of Nematoda responded differently to environmental and habitat-specific parameters. Their functional diversity was higher in alpine sites than for their lowland counterparts [e.g. Pir Panjal Range (Himalaya) (Kouser, Shah & Rasmann, 2021), and Switzerland, European Alps (Kergunteuil *et al.*, 2016)]. In high-elevation habitats, soil-dwelling Nematoda contribute considerably to the soil fauna community and soil food web and therefore play an important role in sustaining ecosystem processes such as carbon and energy flows.

Tardigrades are known to live in extreme habitats and require high humidity, which is why they are mainly found in wet mountainous habitats, such as cryoconite holes (on glaciers) and peatlands, and less often in soil (Zawierucha *et al.*, 2016; Orgiazzi *et al.*, 2016). Rotifers, especially those in the Bdelloidea group, are widespread in the soil and are important contributors to biogeochemical cycling. Like tardigrades, they are highly dependent on soil water (Azzoni *et al.*, 2015) and have been shown to live in the moss and lichen layer on alpine and arctic soils (Fontaneto & Ricci, 2006), surviving unfavourable conditions in a dormant stage. In general, microfauna is favoured in fertile soils with high contents of nitrogen, phosphorus, and organic matter (Devetter *et al.*, 2017) and is easily affected by disturbances such as soil degradation and shrub encroachment after land abandonment (Hu *et al.*, 2017a; Wu *et al.*, 2017a; Wang *et al.*, 2018).

(3) Soil mesofauna

(*a*) *Geographic and taxonomic focus*

Soil mesofauna are mainly composed of springtails (Collembola), mites (Acari), other small arthropods such as Protura, Diplura, Symphyla, and potworms (Enchytraeidae: Annelida) (Potapov *et al.*, 2022). Of these, springtails are the most widespread and abundant invertebrates, occurring in almost all terrestrial ecosystems (Hopkin, 1997; Deharveng, 2004). They play essential roles in many soil ecosystem processes, such as carbon and nitrogen cycling, soil microstructure formation, and plant litter decomposition. Collembola density and diversity vary significantly with environmental factors and plant community composition, and in the shallow alpine soils they inhabit mostly the litter and upper mineral soil layers (Seeber *et al.*, 2021; Xie *et al.*, 2022).

The highest numbers of publications focusing on alpine soil mesofauna were found for Southern & Central Europe (34.0%), Australia & New Zealand (19.6%), and East Asia (15.7%) (Fig. 7, Table S7).

(*b*) *Diversity and drivers of selected mesofauna taxa*

In general, the composition and abundance of soil mesofauna communities is dependent on elevation (Striganova & Rybalov, 2008; Jiang, Yin & Wang, 2015b; Khabir *et al.*, 2015; Schatz, 2017; Winkler *et al.*, 2018), soil properties (van der Merwe *et al.*, 2020), the identity of plant species, and the variability of vegetation communities (Eo *et al.*, 2016; Xie *et al.*, 2022), all of which can lead to high spatial heterogeneity with many local microhabitats. Factors related to climate change, such as temperature (Harte, Rawa & Price, 1996; Alatalo *et al.*, 2017) and reduced soil water availability (Sylvain *et al.*, 2014), as well as (anthropogenic) disturbances may also affect soil mesofauna diversity and communities. Habitat management (Kooch, Shah Piri & Dianati Tilaki, 2021), tourist activity (Meyer, 1993; Kopeszki & Trockner, 1994), cattle trampling and grazing (Hauck *et al.*, 2014; Risch *et al.*, 2015), fire (Driessen & Kirkpatrick, 2017), soil erosion (Meyer, 1993; van der Merwe *et al.*, 2020), and pollution (Rusek, 1993; Visioli *et al.*, 2019), all affect the mesofauna living in alpine grasslands, suggesting that environmental filtering is the predominant process shaping soil mesofauna communities (Visioli *et al.*, 2019).

In the nival zone, the soil fauna community is dominated by springtails and mites, and in some regions (e.g. in the European Alps and the Carpathian Mountains) by predatory false scorpions (Pseudoscorpiones). Potworms, which have high soil specialisation (Anthony *et al.*, 2023) and show high densities in arctic soils (Birkemoe, Coulson & Sømme, 2000; Schlaghamersky & Devetter, 2019), also play an important role in alpine habitats. With increasing elevation, they physically and functionally replace earthworms and can represent a considerable part of the total soil mesofauna biomass (Onipchenko & Zhakova, 1997). Mesofauna distribution in the nival zone is scattered and limited to favourable refugia such as congregations of detritus or cushion plants (Meyer & Thaler, 1995). Some specialist taxa are adapted to snowbeds, which can persist for most of the year (Seeber *et al.*, 2021). These species rely on aeolian food sources (i.e. wind-blown debris landing on the surface of soils, snow, and glaciers) or prey on small animals while searching for this food. Different taxa are active at different times of the day as extreme environmental conditions (e.g. frost) restrict their activity (Mann, Edwards & Gara, 1980; Bauer, 2002). Some specialist species like the potworm *Mesenchytraeus solifugus* (EMERY, 1898) live mainly on snow and glaciers and nearby deglaciated soil in North American high mountains (Smith *et al.*, 1990); the 'glacier flea' *Desoria saltans* AGASSIZ M & NICOLET H, 1841, a springtail from the European Alps, has similar preferences (Potapov, 2001).

(4) Soil macrofauna

(*a*) *Geographic and taxonomic focus*

The majority of studies on macrofauna in alpine mountain soils have been conducted in Central & Southern Europe (58.0%), followed by Central Asia (13.6%). Generic terms only, such as 'arthropods' or 'invertebrates', were used in 33% of all soil faunal publications (Table S7). Elevation and vegetation have been shown to be the primary determinants of abundance and diversity in alpine soil macrofauna communities (Kooch & Noghre, 2020; Steinwandter, Blasbichler & Seeber, 2022; Xie *et al.*, 2022; Lavelle *et al.*, 2022). However, given the wide variety of macrofauna taxa present in soils above the treeline, responses might vary among taxa.

(*b*) *Diversity and drivers of selected macrofauna taxa*

Earthworm (macro-Oligochaeta) diversity shows a hump-shaped distribution along the elevation gradient, with the highest diversity at the treeline (Fontana *et al.*, 2020; Gabriac *et al.*, 2023). Earthworm abundance then decreases in alpine grasslands (Seeber *et al.*, 2005; Steinwandter *et al.*, 2018), likely due to their limited tolerance of the colder temperatures and shallower soil found at higher elevations (Meshcheryakova & Berman, 2014). Additional influencing factors include vegetation attributes such as plant lifeforms and host-plant distributions (e.g. Edwards & Arancon, 2022), as well as soil characteristics such as pH, clay content, 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 occur in dwarf shrub-rich grasslands and ecotones above the treeline, where they can find the mature and stable soils they prefer, as well as more abundant food sources such as fresh plant litter and more degraded organic matter (Onipchenko & Zhakova, 1997; Steinwandter *et al.*, 2018; Gobbi *et al.*, 2020; Kokhia & Golovatch, 2020). Most millipede species reach their upper distribution limit at the ecotone 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 specimens, making estimates of their densities difficult. However, millipedes (and soil invertebrates in general) are more easily and efficiently detected in high-alpine environments by using pitfall traps or hand collecting and are occasionally found at higher elevations [e.g. *Beronodesmoides* spp. (Polydesmida: Paradoxosomatidae) up to 4500 m in Nepal; Golovatch, 2015]. Millipede species inhabiting high elevations mainly belong to the orders Polydesmida, Chordameutida, and Julida (Beron, 2008, 2016). In the European Central Alps, species found at higher elevations belong mainly to Chordeumatida, which are described to be petrophilic with a preference for cold mountain areas and which are active beneath the snow (Meyer, 1980). These millipedes were found in high numbers at sites up to 3000 m (Steinwandter & Seeber, 2023), while other myriapods, such as centipedes (Chilopoda), were almost absent. Other millipede species that frequently inhabit European mountain soils and can be found at high elevation include eurytopic millipede species such as *Ommatoiulus sabulosus* (Linnaeus, 1758) (Julida: Julidae) as well as specialists such as the endemic *Glomeris transalpina* Koch C. L., 1836 (Glomerida: Glomeridae); both are known to inhabit alpine rocky sites and soils even up to 3000 m. Elevational limits may now change with ongoing global warming: Gilgado, Rusterholz & Baur (2021) recently described ten millipede species whose elevational limits in the Swiss Alps have expanded upwards by several hundred metres over the last century.

Ground-dwelling beetles (Coleoptera) and spiders (Araneae), along with other surface-active and highly mobile and agile predators, such as harvestmen (Opiliones) and some beetle (Coleoptera) families, are abundant representatives of the high alpine soil macrofauna (Kaufmann *et al.*, 2002; Hågvar *et al.*, 2020; Gilgado *et al.*, 2022) and seem not to depend on mature soils but rather on available prey and vegetation structure. Numerous studies have investigated the diversity of beetles in mountain soils, but the majority focus on a few widely distributed and well-known families (e.g. Carabidae, Staphylinidae, and Scarabaeidae). The density, diversity, and distribution of predatory beetles are affected by a wide range of factors such as biotic interactions, vegetation (Negro *et al.*, 2010; Yu *et al.*, 2013), abiotic factors such as temperature and moisture (Yu *et al.*, 2013), historical factors such as climatic variability and topographical changes, and human activities (Larsen, 2012; Brandmayr & Pizzolotto, 2016). Topographic isolation also may boost beetle diversity as was found by Armstrong & Brand (2012) above 3000 m on isolated peaks of the Drakensberg (Southern African Ranges), where leaf- (Chrysomelidae), ground- (Carabidae), and sap beetles (Nitidulidae) dominated the soil fauna community (taxa richness and abundance). Research on alpine spiders has been focused on a few families, in particular Lycosidae, Gnaphosidae, and Linyphiidae. Species assemblages are mainly driven by vegetation structure (Malumbres-Olarte *et al.*, 2013) and snowmelt patterns (Hein *et al.*, 2014), with larger species being less sensitive to environmental conditions than smaller ones (Wehner *et al.*, 2023). Particularly high numbers of endemic spider and harvestman species have been described in the European Alps (Komposch, 2010; Paschetta *et al.*, 2016).

Ants (Hymenoptera: Formicidae), as for other soil fauna, decrease in abundance and taxonomic, functional, and phylogenetic diversity with increasing elevation in alpine settings (Glaser, 2006; Machac *et al.*, 2011; Chaladze, 2012; Reymond *et al.*, 2013; Bishop *et al.*, 2014). Elevational limits to occurrence are related to the ability of ants to cope with low temperatures (Bishop *et al.*, 2017). While ant colonies tend to occur in the lower alpine area and become increasingly infrequent in high alpine areas, some individuals (mainly specimens of winged reproductive adults) may be transported upwards by wind. Overall, ant diversity peaks at mid-elevation and decreases consistently – and often linearly – with increasing elevation (Subedi & Budha, 2020). Similar results were found for the Maloti-Drakensberg in Southern Africa by Bishop *et al.* (2014) who attributed the spatial and temporal differences primarily to temperature. In the European Alps, most ant species occurring in the alpine habitat are also present in the higher montane forest belt (Glaser, 2006), and a higher species diversity was recorded in the treeline ecotone (Guariento & Fiedler, 2021). Interestingly, a high number of socially parasitic ant species are reported from alpine habitats without a clear explanation so far, except that the harsher environment might positively select for such life-history traits (Dunn *et al.*, 2009; Schifani *et al.*, 2021). In alpine grasslands, the effect of ants on soils is mostly related to nest construction, since most taxa build their nests in the soil, causing soil turnover as well as nutrient accumulation and influencing the vegetation (Wang *et al.*, 2017b; Zhao *et al.*, 2020b). Ants strategically establish their nests beneath rocks, to benefit from both heat absorption and insulation (McCaffrey & Galen, 2011). Therefore, rock features (e.g. distribution, shape) represent an important factor for the establishment of ant nests. Studies investigating the functional role of ants indicate they occupy higher trophic levels in alpine habitats (Spotti *et al.*, 2015; Guariento, Martini & Fiedler, 2018), even suggesting intraspecific dietary shifts (Guariento, Wanek & Fiedler, 2021).

Larvae of Diptera, especially of lower flies ('Nematocera' such as Tipulidae, Sciaridae, Cecidomyiidae, and Chironomidae) often increase in numbers at higher elevations (Jiang *et al.*, 2015b; Steinwandter *et al.*, 2018). Because they cannot be identified morphologically to species level and are often difficult to extract from soil cores due to low mobility, they are generally a poorly studied soil taxon. They also belong to both macrofauna and mesofauna due to their high size variability. In alpine soils, they can occur in high abundances and – at least in part – carry out crucial soil ecological functions such as litter decomposition and bioturbation which at lower elevations are usually provided by detritivores such as millipedes and earthworms (Meyer & Thaler, 1995; Frouz, 1999; Kitz *et al*., 2015).

(5) Adaptation strategies

Environmental conditions in high-alpine areas can be hostile to animal life, but soil taxa have long adapted and developed strategies to cope with the harsh and varying climate. For example, many taxa (e.g. beetles, spiders, mesofauna) are black, dark brown, or dark grey (Armstrong & Brand, 2012), an adaptation that allows them to absorb sunlight and thus energy better; on the other hand, the metallic appearance of some carabids may function to reflect intense rays of the summer sun. Body appendages are often shorter at higher elevations than those of the same species living at lower elevations, following Allen's rule (i.e. animals in cold climates have shorter limbs). Wing size is also often reduced and there is a higher frequency of brachyptery or winglessness, for example in carabid communities of high-alpine habitats (Pizzolotto *et al*., 2016). Due to the long duration of snow cover, alpine soil invertebrates also typically show increased cold resistance (e.g. *via* antifreeze proteins which delay nucleation in freezing-intolerant species and which inhibit recrystallisation in freezing-tolerant species; Sinclair *et al*., 2003), perform behavioural thermoregulation, and actively seek thermally buffered microhabitats (Dillon, Frazier & Dudley, 2006; Buckley, Ehrenberger & Angilletta, 2015; Schoville *et al*., 2015). Yet, individuals often search for food on the snow surface or in locations that can only be reached by crossing snowfields, increasing the risk of hypothermia. Further, some microfauna can survive being frozen for long periods and have been successfully revived after decades (e.g. tardigrades; Tsujimoto, Imura & Kanda, 2016) and even after thousands of years (e.g. nematodes and rotifers; Shmakova *et al*., 2021).

Besides physiological adaptations, high-alpine soil fauna typically show more generalist diets (i.e. omnivory), presumably in response to the low availability of food resources. Predation seems to be driven by the presence and abundance of given prey. For example, in high-elevation environments such as glacier forefields in Europe (above 2000 m), carabid beetles of *Nebria* spp. and lycosid spiders of *Pardosa* spp. prey on springtails (König, Kaufmann & Scheu, 2011; Sint *et al*., 2019; Hågvar *et al*., 2020), which are specifically associated with the geomorphology of these habitats (i.e. rough stones that can trap food and prevent flushing; Buda *et al*., 2020). Food limitation in such environments also results in simpler and reduced food webs compared to lowland habitats (König *et al*., 2011; Raso *et al*., 2014; Steinwandter *et al*., 2018). In species which are saprotrophic at lower elevations, adaptations to high elevations include the consumption of animal food sources (e.g. exuvia, carcasses, tissue parts) as plant-based litter is rare or absent. For predators such as carabid beetles living in barren high-alpine soils with limited prey availability (mainly springtails), increased intraguild and intraspecific predation has been observed (Raso *et al*., 2014). Additional food can also come from airborne sources, including flying and wind-carried arthropods, as well as detritus (Růžička & Zacharda, 1994; Hågvar *et al*., 2020). Examples of prey interception strategies used by high-alpine taxa include that of the carabid genera *Leistus* and *Notiophilus* which both specialise on hunting springtails; the former *via* trapping them in a setal fence on the ventral surface of the head, and the latter by gauging accurately the distance and direction of the prey before an attack (Bauer, 1985).

Additional adaptations pertain to invertebrate life histories. For instance, life-stage transitions in millipedes and other soil invertebrates (e.g. moulting) can be interrupted and prolonged until spring of the following year if they cannot be completed within a single growing season (Meyer, 1985; Sømme & Block, 1991; Valle *et al*., 2020). Additional examples include parthenogenesis, which is particularly widespread among the soil mesofauna (e.g. springtails and mites) as a reproductive strategy (Pan *et al*., 2023c) or self-fertilisation, which potworms may use in addition to survival as cocoons under cold temperatures (Bauer, 2002).

VII. KNOWLEDGE GAPS AND RESEARCH OPPORTUNITIES

A number of recent papers have discussed knowledge gaps in soil biodiversity science at a global scale (Guerra *et al*., 2020, 2021, 2022). Here we do so for mountain soils and identify research avenues likely to yield important knowledge in support of science-based decision-making, management, and conservation of mountain soils. We place special emphasis on mountain characteristics that are key but also particularly challenging for soil biodiversity research (see Klein *et al*., 2019). These include the typical elevational gradients encountered in mountains, their remoteness, exposure to global change, and their global distribution.

Our literature search indicated that most published research on alpine soil biodiversity has been performed in Central Asia, followed by Central and Southern Europe. All other regions lag far behind (Figs 1 and 8). Equally important biases exist in the taxonomic coverage of the literature, with a disproportionately high number of publications on soil bacteria and fungi, followed by soil fauna (Fig. 8). We also looked at drivers of global change. Amongst the 683 publications mentioning direct drivers of change, almost 50% address climate change, followed by land-use change and pollution. Despite the growing recognition of the ecological

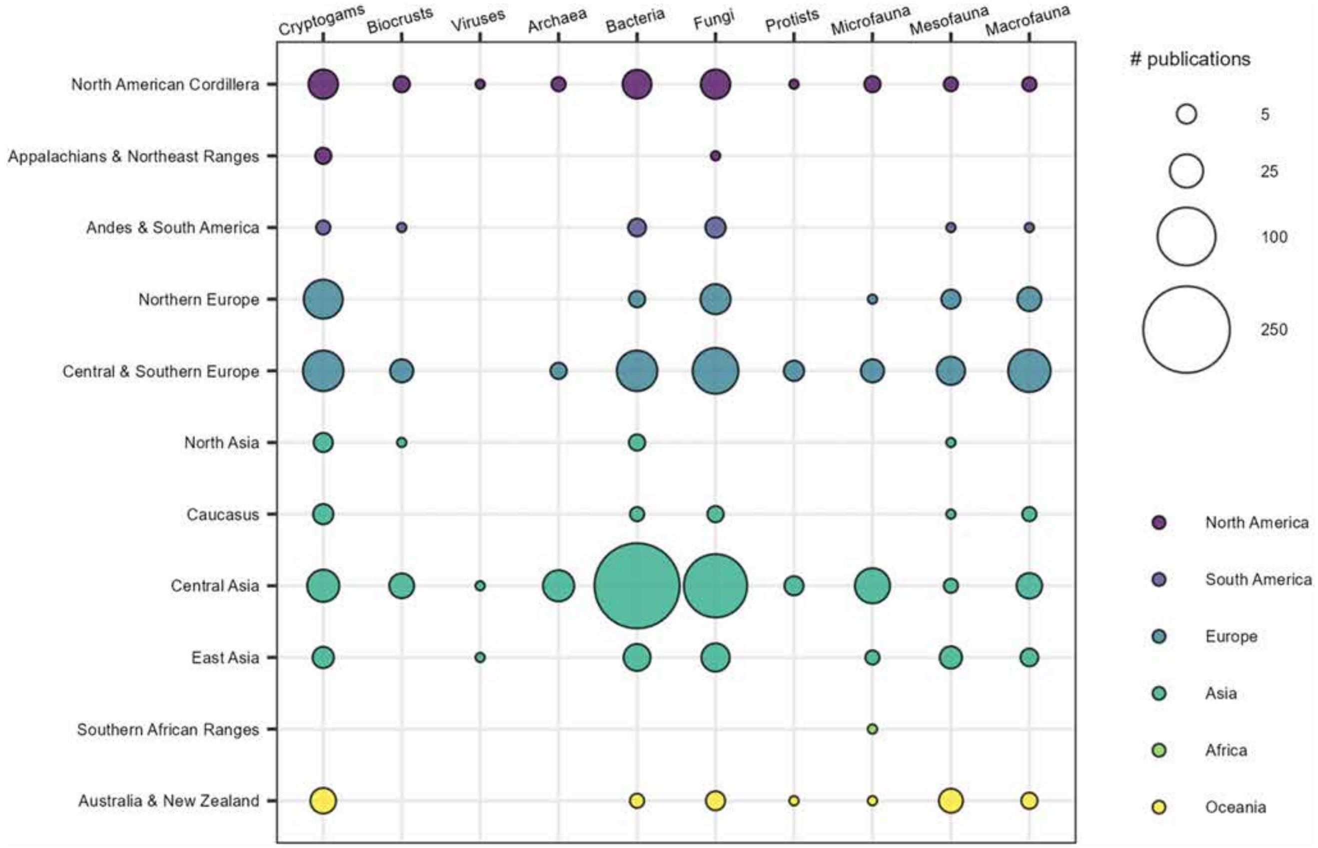


Fig. 8. Taxonomic and geographic distribution of studies in temperate and continental mountain soil biodiversity research above the treeline. The number of studies include those where the organismal group was either the primary or secondary focus of the study.

impacts of invasive species, only 22 published (3.2%) studies had a focus on biological invasions in alpine soils (data not shown). Thematically, our analysis shows that a clear majority of studies, in particular microbiota studies, are within the fields of community ecology (biotic communities and interactions), ecosystems ecology (ecosystem functioning), and biogeography (Fig. 9), leaving many research questions in conservation biology, population dynamics, or behavioural ecology unaddressed.

(1) Increase and improve mountain soil biodiversity data across organismal groups and locations

Research on mountain soil organisms has increased in the last decades (Fig. 3). This is particularly the case for bacteria and fungi, as recent advances in DNA-based technologies have facilitated rapid collection of data. However, in line with recent global analyses (e.g. Dainese *et al.*, 2024), our synthesis points to geographic and taxonomic gaps and biases in mountain soil biodiversity data and research. In particular, there are limited data for groups such as soil fauna that have been described more exhaustively from 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. There may be species on the verge of extinction and/or critical in supporting high-alpine ecosystems that are still overlooked by science, conservation, policy, and advocacy. As critical soil organisms, rare species, and/or keystone species disappear, the functioning of entire ecosystems could be disrupted, with consequences for nature and people (Jousset *et al.*, 2017; Banerjee, Schlaeppi & van der Heijden, 2018; Chen *et al.*, 2020a; Guerra *et al.*, 2021). The relative lack of species-level identification and the limited number of publications on biological invasions both imply a risk of overlooking invasive species that may alter soil properties or represent a threat to native species and their functions [e.g. the earthworm *Amynthas agrestis* (Goto & Hatai, 1899) in the Great Smoky Mountains (Appalachian Mountains); Snyder, Callaham & Hendrix, 2011]. Furthermore, limitations in spatial representativeness and coverage of taxonomic groups in soil biodiversity data constrain our capacity to understand mountain soil systems and their response to change based on comparative analyses at multiple biogeographic scales.

In addition to the absence of information on the existence of many species, limited long-term data on spatio-temporal trends in populations, species distributions, and community composition further jeopardise the ability of science and policy to detect, interpret, and ultimately address or prevent

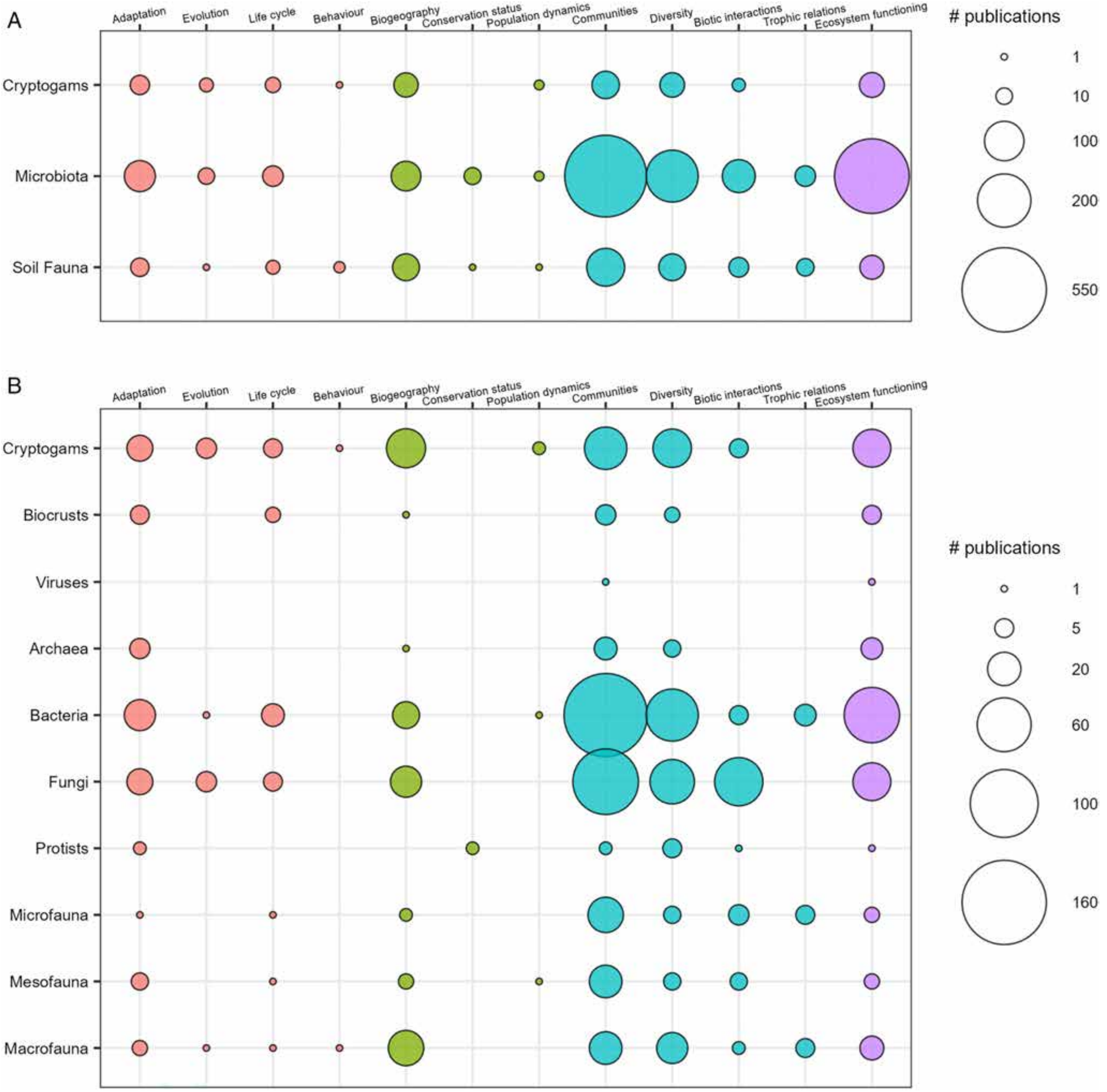


Fig. 9. Frequencies of main research focus on the three main soil organismal groups, including all specific and generic mentions of cryptogams, microbiota, and fauna (A) and on specific taxa within these groups (B) as reported in the corpus of literature on biodiversity in mountain soils above the treeline. Research focus is a category in the custom thesaurus. For each paper, the main research focus is the one with the highest count of corresponding key words extracted from the title and abstract (see Appendix S1: Material and Methods). The numbers of studies include those where the organismal group was either the primary or secondary focus of the study.

effects of global change on mountain soils and ecosystem functions. While species distribution and range expansions have been increasingly well documented for some taxonomic groups such as plants (e.g. Rumpf *et al.*, 2018; Staude *et al.*, 2022), temporal variation in diversity along elevational, topographical, or other ecological gradients is largely unknown for soil organisms [e.g. see Seppey *et al.* (2020) for soil protists]. Importantly, these gaps in knowledge also hamper the establishment, design, and prioritisation of future monitoring efforts as well as the integration of soil biodiversity into Red Lists of threatened species.

We support previous calls for better geographic and taxonomic coverage in soil biodiversity research and for prioritising long-term monitoring of life in mountain soils at national (Guerra *et al.*, 2020, 2021; Eisenhauer *et al.*, 2022) and global (Maestre & Eisenhauer, 2019) scales. Multiple options exist for increasing and improving mountain soil biodiversity data (see also Hochkirch *et al.*, 2021). One is the use of molecular approaches such as DNA or RNA barcoding and the use of metagenomics and metatranscriptomics. These methods offer great opportunities, in particular for the detection and identification of microbiota (e.g. Guerra *et al.*, 2021). While already in use for bacteria and fungi (see Section V), DNA-based technologies could also provide useful information for other soil organisms in mountains. However, the assignment of molecular data to species remains a limitation across taxonomic groups and ecosystem types (e.g. Recuero, Etzler & Caterino, 2024; Le Cadre *et al.*, 2024; Weigand *et al.*, 2019). One option to increase species discovery rates would be the identification of mountain locations where unknown taxa are most likely to be encountered (e.g. Delgado-Baquerizo, 2019; Verdon *et al.*, 2023). Such efforts may be especially useful in remote mountain locations where fieldwork is particularly challenging and would benefit from available information on species distributions from related taxa. Similar approaches include the identification of sampling locations based on the intersection of spatial data sets of mountain extents (Snethlage *et al.*, 2022a), key environmental variables known to determine distribution patterns, and abiotic factors (e.g. soil temperature and type). Furthermore, as suggested by van der Putten *et al.* (2023), an alternative to identifying species is to investigate soil biota based on traits in order to understand what ecosystem functions are likely to be lost as species go extinct. A trait-based approach could be particularly interesting in mountains where harsh environmental conditions, including extreme temperature (gradients) and biophysical stressors such as recurrent avalanches, likely determine unique sets of traits.

(2) Improve detection and prediction of global change effects on mountain soil biodiversity

According to the literature we summarised, the occurrence and diversity of life forms in mountain soils is directly determined by temperature, snow cover, precipitation, humidity and wind, as well as factors such as soil properties (e.g. pH, organic matter quantity and quality, parental material composition). Accordingly, in the face of global change, soil communities are expected to experience novel life conditions influencing their distribution, dynamics, survival, and functions (e.g. Feng *et al.*, 2023b). For those soil organisms whose ecology and life histories are tightly associated with plants, additional impacts of climate change can be expected as the elevation range limits, distribution, and community composition of vascular plants changes. Finally, as environmental factors such as temperature and soil moisture determine not only the occurrence and diversity of organisms but also specific biochemical cycles such as the production of methane (e.g. Hofmann, Reitschuler & Illmer, 2013), feedback loops are likely to magnify effects of climate and land-use change and thereby exacerbate the exposure of soil biota to unprecedented and extreme environments. Such feedback loops and cascading effects are likely to be exacerbated by the numerous reciprocal effects of organisms on their environment (e.g. pedogenic effects of cryptogams; Musielok *et al.*, 2021).

Detecting and predicting the impacts of global change and anthropogenic activities on mountain soil biodiversity will be essential to formulating effective conservation and management measures and thereby safeguarding soil functions, services, and health (Arora, 2023). In that context, and in line with existing efforts such as the SoilTemp project (Lembrechts *et al.*, 2020), improving the spatial resolution, temporal coverage, and accuracy of ongoing measurements of key environmental factors could enable better predictions and prevention of ecosystem degradation and species loss. We join others (e.g. Bouaicha *et al.*, 2022; Eisenhauer *et al.*, 2022) in calling for improved data and remote-sensing efforts for less-common drivers of soil biodiversity change, such as pollution by microplastics, chemicals, and heavy metals. Such data are particularly important in mountain regions, where global atmospheric transport of micropollutants as well as human activities are major historical (e.g. Le Roux *et al.*, 2020) and current sources of pollution (Schmeller *et al.*, 2022). As exposure to anthropogenic factors typically varies across seasons (e.g. pastoralism in the summer and ski runs in the winter), improved data will be important to identify and understand global change drivers and their interactions, both in space and time. Moreover, given the high level of interactions between soil organisms, understanding and predicting the responses of soil biota to global change calls for the joint monitoring and analysis of multiple groups and species and their interactions with each other and their environment (Eisenhauer *et al.*, 2022). We further recommend that global change research in mountain soils follows a comparative approach that takes advantage of the fact that mountains are distributed worldwide (Körner *et al.*, 2017; Snethlage *et al.*, 2022a) but differ in their environmental conditions, their history of exposure to human pressure, as well as in their environmental gradients. For example, exposure to high temperatures and extreme dryness currently is more common for certain ranges, such as in the Mediterranean or inner European Alps, where soils and their biota show specific community composition and species adaptations (Praeg *et al.*, 2020). Accordingly, comparative analyses of soil biodiversity – including genetic and trait diversity – as well as niche properties are likely to yield useful information with respect to the evolutionary potential of both individual species and terrestrial ecosystems (Bardgett & van der Putten, 2014) in the face of global change and to mitigation strategies and conservation priorities (e.g. Mod *et al.*, 2021). Biogeographic studies, palaeoecological analyses, and research in under-studied fields such as evolutionary and behavioural ecology will provide useful information on the distribution of species over evolutionary time and on the resilience of mountain soils to changes in climate.

(3) Prioritise mountain soils in policy and conservation

Belowground biodiversity is essential to healthy soils, which in turn are crucial for food production, aboveground biodiversity, climate control, and human health and security (Banerjee & van der Heijden, 2023). However, despite their importance, mountain soils and their biodiversity remain only poorly addressed in laws, restoration, and conservation policies (but see Stanchi *et al*., 2023). The observation that most parties to the Convention for Biological Diversity (CBD) have no national target explicit to soil conservation and biodiversity (Guerra *et al*., 2021) and that the protection and conservation of soil biodiversity and soil ecosystem functioning has been insufficient to date (Zeiss *et al*., 2022) also applies to mountain soils. One of the challenges associated with soil conservation and protection, as well as with the formulation of laws and guidelines for the sustainable use of soils, is that soils are connected across national borders and continents by human activities (e.g. international trade, tourism) (van der Putten *et al*., 2023). This calls for international agreements such as the Soil Conservation Protocol, as well as for reinforced international collaborations, such as those established within the Soil Working Group of the Alpine Convention. Another challenge that contributes to making mountain soils and the diversity of species they host a blind spot in science, conservation, and policymaking is associated with the difficulties of data collection in remote and steep environments.

We support ongoing efforts (e.g. Guerra *et al*., 2021; Arora, 2023; van der Putten *et al*., 2023) to raise the importance of soil biodiversity in environmental policies and formulate frameworks for the protection and restoration of soils (e.g. 'EU Soil Strategy for 2030' and the associated 'Soil Monitoring Law'). However, given the critical importance of healthy and biodiverse soils in mountains (e.g. for natural risk regulation), we also call for dedicated efforts and explicit political commitments towards their targeted protection. The ongoing development of National Biodiversity Strategies and Action Plans in response to the adoption of the Kunming–Montreal Global Biodiversity Framework represents a unique opportunity to collaborate on the formulation of soil biodiversity conservation targets as well as indicators applicable to mountain ecosystems (Guerra *et al*., 2021). In support of such developments, we reiterate previous calls (Maestre & Eisenhauer, 2019; Guerra *et al*., 2021, 2022) for improved monitoring of soil biodiversity and soil-related essential biodiversity variables in mountains (Schmeller *et al*., 2024) as well as for the systematic evaluation of the efficiency of protected areas in preserving mountain soil species and their functions (see e.g. Ciobanu *et al*., 2019). In addition, we further call for reinforced collaborations with international initiatives such as SoilBON, the Global Soil Biodiversity Initiative, and the Global Soil Partnership of the United Nations Food and Agriculture Organisation (e.g. Stanchi *et al*., 2023). Besides political commitments and increased scientific efforts, awareness raising and education through effective communication methods (e.g. Steinwandter & Seeber, 2022) remain essential on our path to safeguarding all kind of soils, including mountain and alpine soils.

VIII. CONCLUSIONS

(1) We synthesised published research and expert-based knowledge on cryptogams, soil microorganisms, and soil fauna in temperate and continental alpine soils above the treeline.

(2) Our analysis of mountain soil biodiversity literature shows a distinct acceleration in the number of publications on alpine soil biodiversity in the last decade, with the most notable increase in studies on alpine soil fungi and bacteria, while research on cryptogams and soil invertebrates has grown at a slower pace. Thematically, most studies to date have focused on community ecology and diversity, particularly in the context of climate change, followed by a focus on land-use change and pollution, thereby reflecting the most pressing current questions in ecological research.

(3) Our expert-based synthesis of the literature documents the complex interplay of soil environmental, climatic, and anthropogenic drivers determining mountain soil biodiversity patterns across organismal groups. We also document a systematic decrease in biocrusts and invertebrate diversity with increasing elevation, with cryptogams first increasing and then decreasing towards the nival belt, and, thus, confirm the key role that elevation plays in shaping the biodiversity and distribution of these organisms in mountain soils. The response of archaea and bacteria to elevation is more diverse, although also dictated by soil conditions and climate, whereas for fungi associations with vegetation play a pivotal role. This synthesis provides a unique overview of the remarkable diversity of soil organisms in mountain regions and identifies some of the adaptations that allow them to exist at high elevations.

(4) Our analysis of the existing literature highlights the need to address spatial, taxonomic, and thematic biases in mountain soil biodiversity research. Dedicated efforts are needed in understudied regions such as the Americas, the Caucasus, and the Southern African ranges, and in scaling up data collection for biocrusts and invertebrates, for which we have limited data available in comparison to microbiota. We also need to improve functional knowledge for protists, invertebrates, and the vast majority of uncultivated prokaryotes and fungi, for which functional or ecological descriptions are lacking. We recommend increased efforts to collect data on the biodiversity of mountain soils to improve our ability to predict the impacts of global change on these soils. Improving our knowledge of genetic and trait diversity to assess evolutionary responses could further enhance our understanding of the impacts of global change on mountain soil organisms.

(5) Our review recommends clear political commitments towards the protection and conservation of mountain soils,

improved international collaboration, and the incorporation of mountain soil biodiversity in global policy frameworks. We equally stress the importance of awareness-raising and education to promote the conservation of mountain soils.

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X. DATA AVAILABILITY STATEMENT

The data set generated and analysed is available from the public repository Zenodo (DOI: 10.5281/zenodo.15147939).

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XII. SUPPORTING INFORMATION

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

Appendix S1. Detailed description of the methodology, statistical analyses, and additional results.

Appendix S2. Publications identified by our search string for which a target organismal group could be extracted and georeferenced (mountain or country).

Appendix S3. ZIP-file containing the full reference list in BibTex, RIS, and CSV formats.

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