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REVIEW

Effects of reduced snowpack due to climate warming on abiotic and biotic soil properties in alpine and boreal forest systems

Anastasiia Kosolapova, Ianina Altshuler*

MACE Laboratory, Environmental Engineering Institute (IIE), Alpine and Polar Environmental Research Centre (ALPOLE), School of Architecture, Civil and Environmental Engineering (ENAC), École Polytechnique Fédérale de Lausanne (EPFL), Lausanne, Switzerland

* ianina.altshuler@epfl.ch

Abstract

Reduction in snow cover, depth, onset, and duration of seasonal snow in mid-latitude regions due to climate warming has multiple global and local scale ecosystem impacts. These effects include modulations of the hydrological cycles and increases in land surface solar radiation absorption due to decreased albedo. Changes in snow cover characteristics also affect underlying soils. Snow has an insulating effect on soils by decoupling air and soil temperatures, thus seasonal snow cover reduction leads to overall lower soil temperatures and an increase in freeze-thaw cycles. This is especially prominent during the fall and spring thaw seasons when the snow cover is not as extensive. This in turn has downstream impacts on soil physical, chemical, and biological properties. Among these impacts are soil moisture reduction, temperature, frost regimes, soil pH shifts, and alteration in nutrient flux dynamics during winter, snowmelt period and the following summer growing season. These changes in soil physicochemical properties due to snowpack reduction can then impact the biological soil properties via increased plant root mortality, reduced abundance and diversity of soil arthropods, and shifts in composition, abundance and activity of soil microbial communities. All these soil biotic factors can in turn alter the dynamics of soil nutrient fluxes and future greenhouse gas emissions. Here, we integrate data on the effects of snow cover reduction on abiotic and biotic soil properties, with focus on temperate alpine and forest ecosystems and with an outlook on future impacts.

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1. Introduction

In temperate and mountain ecosystems, seasonal snow covers the ground from several weeks to months during the cold season [1]. In the Northern Hemisphere, up to one-third of the land area is covered with snow for at least three months per year [2–4]. Seasonal snowpack is highly sensitive to climate change, with warming being a major factor affecting seasonal snow cover [1]. Snow cover extent has decreased by 13% per decade for the last fifty years and continues to decrease across the Northern Hemisphere [5,6], while the duration of the snow cover period is also declining, mainly due to the earlier onset of snowmelt [7,8]. Moreover, since 1950's the overall mean and maximum snow depths have reduced across Europe, including mountainous regions, with the acceleration of the trend after the 1980's (with notable exception at the higher latitudes) [9–11]. Warmer winter temperatures and the increase in precipitation, both due to climate change, have opposing effects on seasonal snow cover [9]. However, increase in winter precipitation appears to have a significant impact on snow cover in high-altitude areas, whereas in mid- and low-altitude regions, temperature has the principal impact on snow cover [12].

Seasonal snow cover has multiple effects on these ecosystems contributing to energy balance by cooling the Earth's surface and reducing ground heat losses [13]. Firstly, as snow has a high surface albedo, it reflects 60–90% of solar radiation (lower values for wet spring snow) [14–16], resulting in lowering of the surface temperature [17,18]. Secondly, snow has a low thermal conductivity [19] which allows the snowpack to act as an insulator, decoupling underlying soils from freezing air temperatures and reducing heat loss from the ground [15]. The stable snow cover decreases the fluctuations in soil temperatures and minimizes the number of soil freeze-thaw events [20]. This, in turn, influences the activity and viability of soil-inhabiting organisms throughout the cold season and has downstream impacts during the growing season [21,22]. Another major effect of the seasonal snowpack on ecosystems is its role in hydrological cycles as it acts as a seasonal water reservoir. In the Northern Hemisphere, snowmelt water is dominate source of runoff [23], recharging freshwater and groundwaters resources [24,25]. On local the scale, meltwater is a source of moisture and nutrients for the underlying soil [2], thus the timing of snowmelt affects the growing season productivity and activity of the soil microbiome [26,27].

Here we review the effect of climate change on the seasonal snow cover with focus on temperate and mountain ecosystems, while still utilizing knowledge from higher latitude habitats. In addition, we focus on the impacts of reduced seasonal snow cover on the underlying soils in the context of their physical and biogeochemical properties as well as soil-associated biomes.

2. Effects of snow cover reduction on physical properties of soils

Seasonal snow cover has a significant influence on underlying soil physical characteristics, mainly soil temperatures [15,28]. The key property of the snow affecting soil temperature is snow's low thermal conductivity [19]. Low thermal conductivity makes snow an excellent insulator decoupling the atmosphere and ground surface, which in turn lowers the impact of air temperature on the soil thermal regime. The magnitude of the snow insulation effect varies with the extent of snow cover, depth, density and structure, timing, and duration of the seasonal snow cover [15]. Snow depth is one of the major factors affecting the soil thermal regime during the cold season. The insulating effect of snow is greater in thicker snowpack [15,29], with complete decoupling of ground and atmosphere occurring at around 30–40 cm of snow [30]. In addition, late season dense/melting snow has greater thermal conductivity compared to fresh early winter snow [15,29]. Timing of snow cover deposition is important, as areas where snow cover is established before ground freezing, the snow insulating effect allows soil temperature to be maintained above 0˚C, i.e., the soil remains unfrozen throughout the winter [31].

With climate warming, snow cover undergoes reduction in spatial distribution, reduction in depth, delayed deposition, and earlier snowmelt [32–34]. Snow cover reduction leads to greater exposure of soil to cold air temperatures which may result in "colder soils in a warmer world" and increase soil freezing [22,35] (Fig 1). This leads to reduced liquid water availability in winter soils [36] and reduced solute infiltration rates during the snowmelt period [2,37]. The thinner snowpack or its complete absence also may lead to a greater amplitude of soil

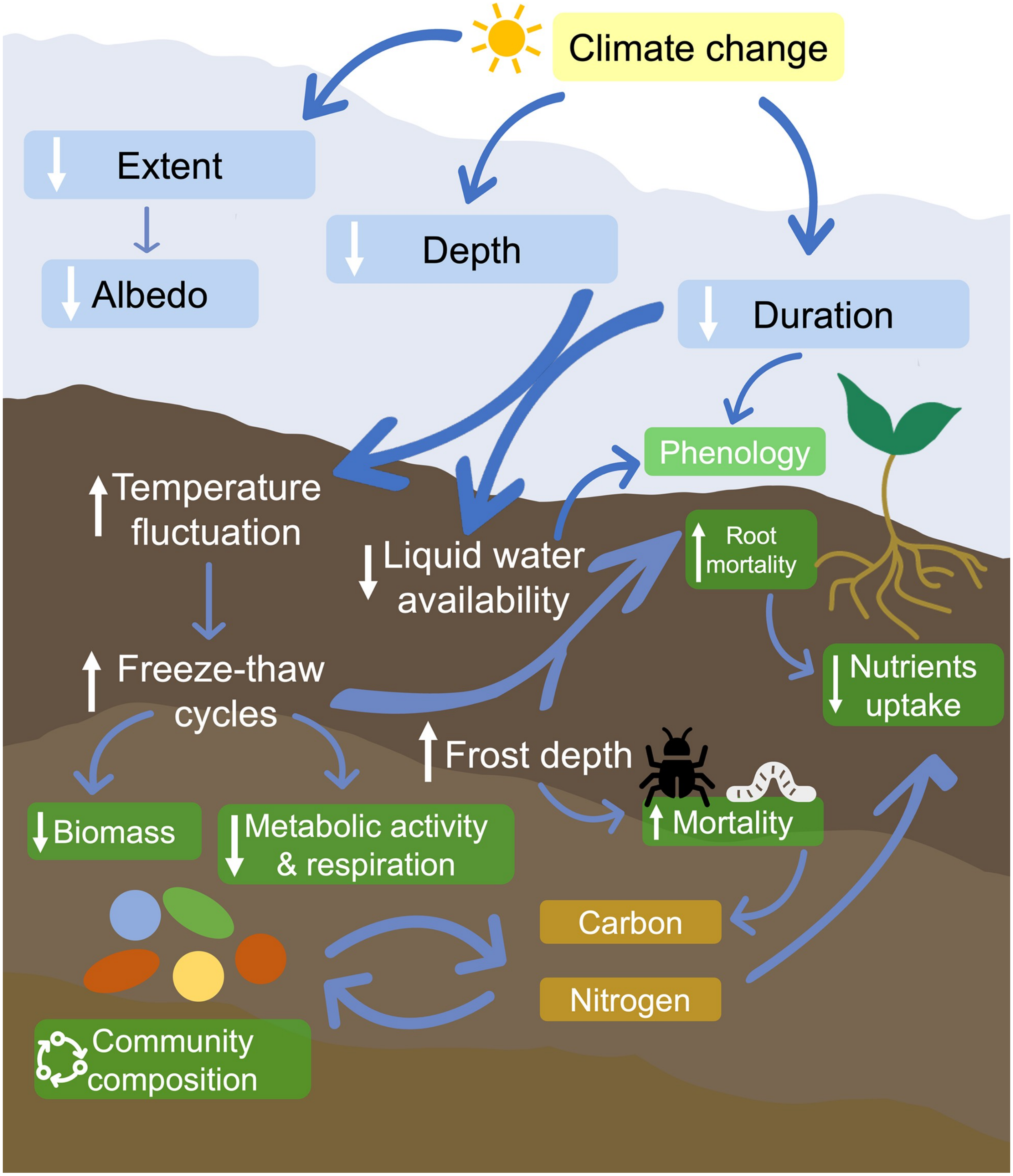

Fig 1. Snow cover reduction and its effect on soil biome.

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temperature fluctuations throughout the cold season and an increased number of freeze-thaw events [38,39], due to the lack of the decoupling from air temperatures. For example, to simulate a reduction in snow cover depth due to climate warming, Broadbent et al. (2021) conducted snow removal experiments in the European Alps, demonstrating an increased number of freeze-thaw events in plots with shallower snow depth [40]. Similar results were obtained in snow removal experiments conducted in the alpine forest ecosystem of the Tibetan Plateau [41,42].

3. Snow manipulation experiments

To assess the effects of snow cover reduction on underlying soils several overarching strategies are possible, including i) sampling of naturally heterogeneous snow accumulation sites [43], ii) long-term monitoring [44], iii) snow manipulation experiments which are the most utilized approach in ecological and biogeochemical studies assessing the impacts of climate change [45]. Snow manipulation experiments can include snow addition, partial or full snow removal, and snow compaction [45]. Snow removal plots are created by either manual periodical snow removal or physical cover of the experimental plot which prevents snow accumulation [41,46]. Another manipulation approach is the installation of a snow fence, that alters snow accumulation creating a snow depth gradient with zones of deep, moderate, and shallow snowpack [47,48].

Several reviews and meta-analyses were published in the last 15 years summarizing the results of snow manipulation experiments, including a review by Wipf and Rixen (2010), focused on snow manipulation experiments in Arctic and alpine tundra ecosystems from a plant phenology perspective [49], and a meta-analysis by Zhao et al. (2022), summarizing results of 99 snow manipulation experiments with the focus on physicochemical characteristics and biotic properties of soil [45]. However, direct synthesis of data obtained through snow manipulation experiments results is complicated as there is heterogeneity in experimental designs (snow manipulation strategy and sampling timing), as well as heterogeneity in the type of analyzed soil properties.

Alpine habitats are highly sensitive to warming and subsequent greening with spatial, temperature, and snow cover heterogeneity resulting from steep altitudinal gradients [50,51]. To draw conclusions of the effects of snow cover changes with climatic warming in these sensitive habitats, we summarize the results of snow manipulation experiments in subalpine and alpine ecosystems with focus on soil biogeochemical properties and effects on the soil microbiome (Table 1).

In most of the studies performed in subalpine and alpine environments, snow removal consistently resulted in decreased soil temperatures during the winter, increased frost formation in topsoil, and an increase in the number of freeze-thaw cycles (Table 1). However, some of the studies have not detected any significant influence of snow removal on these characteristics. For example, Bombonato and Gerdol (2012) conducted a study in the European Alp peatland, where they removed snow only once in late winter/early spring, which resulted earlier snowmelt but had no effect on soil temperature or frost formation [52]. Contrariwise, Gavazov et al. (2017) conducted a similar snow removal experiment at the same elevation in the European Alp grassland, again snow was removed only once in the late winter, however, this led to increased frost formation in soil [36]. This difference can potentially be explained by higher spring air temperatures or ecosystem type in the experiment performed by Bombonato and Gerdol [52].

Overall, across the studies, snow removal experiments performed in subalpine and alpine environments have not demonstrated any clear and unified effect on the geochemical

Table 1. Snow removal experiments conducted in subalpine and alpine ecosystems.

Author, year	Locat.	Elevat., m.a.s.l.	Ecosystem	Mean annual air T,˚C	Annual precipitation, mm	Experimental design/strategy	Soil sampling period	Physical effect	Geochemical effect	Biological effect
Bombonato, Gerdol, 2012 [52]	European Alps	1800	Peatland	~3.0	~1000	Snow was **manually** removed **one time** either in late winter or early spring. Plot size = 1.5 m^2	Growing season (June, July, September)	No effect of snow removal on soil temperatures during the snow season. Earlier snow melt in snow removal plots.	No significant effect on DOC, DTP, DTN, DTN: DTP in snow removal plots.	No effect on microbial respiration in spring and summer in snow removal plots.
Freppaz et al., 2008 [46]	European Alps	1450	Subalpine grassland and under larch site	4.0	1070	Snow was **manually** removed **multiple** times (2 days after each snowfall). Plot size = 100 m^2	From October to March	Frequent freeze-thaw events and mild freezing in snow removal plot.	Increase in net ammonification (both ecosystems: 459.67% under larch) and increase (78.16%) in net nitrification (meadow) in snow removal plots.	Decrease in MBC (meadow) and no effect on MBN in snow removal plots.
Broadbent et al., 2021 [53]	European Alps	2650	High alpine grassland	−0.3	860	Snow was **manually** removed **four times** in spring. Plot size = 25 m^2	6 time points: from late winter to early summer	Earlier onset of the snowmelt in snow removal plots.	Earlier decline in available NH_4^+	Earlier decline in bacterial biomass and community composition and decrease in biomass-specific urease activity in snow removal plots.
Broadbent, et al. 2022 [40]	European Alps	2472	High alpine grassland	3.2	885	Snow was **manually** removed **three times** in late winter early spring. Plot size = 4 m^2	Growing season (July)	Increase in freeze-thaw cycles in the plots with removed snow.	Lower soil C in snow removal plots (9% - 17.7% decrease).	Snow removal had no effect on total bacterial or fungal abundance and led to lower in situ soil respiration (16.1% -31.82% decrease). Doubled abundance of *Bacillaceae* family in snow removal plots.

(*Continued*)

Table 1. (Continued)

Author, year	Locat.	Elevat., m.a.s.l.	Ecosystem	Mean annual air T,˚C	Annual precipitation, mm	Experimental design/strategy	Soil sampling period	Physical effect	Geochemical effect	Biological effect
Gavazov et al., 2017 [36]	European Alps	1820	Subalpine grassland	NA	NA	Snow was **manually** removed **one time** in mid-winter. Plot size = 4 m^2	4 times throughout the winter	Topsoil freezing in snow removal plot.	Snow removal has no effect on soil extractable organic N and DOC.	Snow removal led to microbial biomass reduction (23.14% decrease). Snow removal has no influence on respiration and community composition. Soil communities had higher proportion of bacteria in winter.
Robroek et al., 2013 [54]	Jura mountains	1036	Peatland	<5.0	1,500	Snow was removed **manually** once **every three weeks**. Plot size = 1m^2	Chemistry: from March to May. Microbial biomass: April	Earlier soil thaw and higher rate of soil temperature fluctuation in snow removal treatment.	No significant effect of snow removal on DOC and other major nutrient concentrations.	No effect of snow removal on soil microbial biomass. Induced fungal growth in snow removal plots.
Freppaz et al., 2012 [48]	Rocky Mountains	3528	Alpine grassland	-3.8	1006	**Snowfence** (60 m long) was installed to create gradient of snow depth with deep, moderate, shallow snow zones.	Growing season (September)	NA	Decrease in snow depth led to increase in pH and decrease in TOC (-33.38%), TN (-37.37%), NH_4^+(-49.19%), NO_3^- (-52.2%). Decrease in TN and TOC in shallow snowpack zone compared to before snow fence installation (1993).	Decrease in MBC (-35.68%) and MBN (-38.52%) in shallow snow zone.
Ade et al. 2018 [55]	Tibetan Plateau	3485	Alpine grassland	1.1	ND	Experimental plots were **covered** with **tarpaulin** to prevent snow accumulation. Plot size = 4 m^2	Growing season (August)	No significant difference in soil temperatures.	Decrease in AP (-22.3%), TP (-3.66%), and TOC (-9.41%). Increase in TN (9.32%)	No significant differences in alpha-diversity and communities composition; No significant difference in beta-diversity.

(*Continued*)

Table 1. (Continued)

Author, year	Locat.	Elevat., m.a.s.l.	Ecosystem	Mean annual air T,˚C	Annual precipitation, mm	Experimental design/strategy	Soil sampling period	Physical effect	Geochemical effect	Biological effect
Li, Z. et al. 2017 [41]	Tibetan Plateau	3021	Alpine forest	3.0	850	Plots were **covered** with **wooden roofs** to prevent snow accumulation. Plot size = 9 m^2	Early snow, deep snow, snowmelt periods.	Lower soil temperature (decrease by 1.44˚C on the surface and by 0.33˚C at 5 cm depth), increased number of freeze-thaw events, deeper soil frost, but decrease in frost duration in snow removal plots.	Increase in inorganic N (26.56% in winter, 48.1% during snowmelt) and DON (75.78% in winter, 39.38% during snowmelt) in snow removal plots.	Snow removal has no influence on MBN, but led to increase in MBC in winter (40.94%) and reduced enzymatic activities (18.63% decrease in urease activity, 29.67% decrease in nitrate reductase activity, 13.57% decrease in nitrite reductase activity).
Ren et al. 2020 [56]							Deep snow, snowmelt, growing season.	Increase in number of freeze-thaw events and lower winter soil temperatures in snow removal plots.	ND	Snow removal led to higher alpha-diversity and differences in microbial community composition compared to non-manipulated control plot during deep snow period.
Yang, K. et al. 2021 [42]							Early thawing period	More freeze-thaw events and lower soil temperatures in snow removal plots.	ND	Decrease in total PFLA (26.95% - 28.7%) and bacterial PLFA (27.12% - 28.26%) in snow removal plots.

(*Continued*)

Table 1. (Continued)

Author, year	Locat.	Elevat., m.a.s.l.	Ecosystem	Mean annual air T,˚C	Annual precipitation, mm	Experimental design/strategy	Soil sampling period	Physical effect	Geochemical effect	Biological effect
Tan, B. et al. 2014 [57]	Tibetan Plateau	3580	Alpine forest	3.0	850	Plots were **covered** by **roof with plastic film** cover (80% transparency to light) to prevent snow accumulation. Plot size = 10 m^2	7 times from before snow fall, winter, snowmelt, early growing season.	Snow removal led to increased soil freezing and decrease in mean and minimal soil temperatures	Snow removal led to decrease soil moisture in winter, increase in nitrate (366.79% in late winter; 87.52% during snowmelt), DOC (86.79% in late winter) and DON (259.99% in late winter; 149.95% during snowmelt).	Increase in MBC:MBN ratio (76.13%) in winter in snow removal plots. MBC was decreased in early snow cover (16.92%), higher in snowmelt (56.85%) and early grow (21%) in snow removal plots. MBN was lower in early snow cover (52.91%), higher in deep snow (32.88%) and snowmelt (102.99%) in snow removal plots. Snow removal led to decrease in urease (56.94%) and invertase activity (32.24%) in late winter.
Yang, F., et al., 2021 [58]	Tibetan Plateau	3579	Alpine forest	2.7	850	Plots were **covered** with non-transparent **PVC roof** to prevent snow accumulation. Plot size = 1 m^2	Early, deep snow, snowmelt periods.	Snow removal led to increased fluctuations in soil temperatures.	DOC decrease (50.2%) in mineral soils and DON decrease (24.59%) in organic soils in snow removal plots in early winter.	No significant effect on microbial biomass and enzyme activity in response to snow removal.

Locat., location; Elevat., elevation; NA, not available; DOC, dissolved organic carbon; DTP, dissolved total phosphorus; DTN, dissolved total nitrogen; DON, dissolved organic nitrogen; MBC, microbial biomass carbon; MBN, microbial biomass nitrogen; TN, total nitrogen; TOC, total organic carbon; AP, available phosphorus; TP, total phosphorus.

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properties of soils (Table 1). This mostly originates from the limited number of available works and a diversity of measured chemical parameters. In the meta-analysis performed by Zhao et al. [45], snow removal had a significant effect only on ammonification and nitrification rates in winter soils, though only a few works have analyzed these parameters [46]. In the growing season, Zhao et al. revealed a significant increase in C, DOC, NH_4^+ and DON, though these results face the same problem, as the measurements of these parameters were available only for a very limited number (2–3 experiments) of studies [45]. However, alpine centric studies (Table 1) overall do not align with these conclusions. For example, Bombonato and

Gerdol (2012) demonstrated no effect on DOC [52], and Freppaz et al. (2012) exhibited that in zones with reduced snow cover (via snow fence manipulation) there was a decrease in TN (37.37%), NH_4^+(49.19%), TOC (33.38%) in alpine grassland of the Rocky Mountains [48]. From a biological perspective, snow removal often resulted in a reduction of microbial biomass and enzymatic activity, as well as a shift towards higher abundance of fungal taxa in winter soil microbial communities (Table 1) (see section 4). For example, both Freppaz et al. (2012) and Gavazov et al. (2017) demonstrated loss of microbial biomass in snow reduction experiments [36,48].

In order to estimate overall effect of snow cover reduction on different soil geochemical and biological properties in alpine ecosystems, we quantitatively synthesised available data from studies focusing on snow removal experiments in alpine (high-altitude) ecosystems (Supplementary Table 1). Overall, we extracted data from six studies performed in Tibetan plateau [41,42,55–58] and two studies performed in the European Alps [40,53]. The majority of studies performed in Tibetan plateau were performed in alpine forest ecosystem [41,42,56–58] whereas all studies from the European alps were performed in high alpine grasslands [40,53]. To estimate the magnitude of the observed effects we calculated log response ratio (lnRR) [59], the most-used effect size metric for assessment of ecological studies results [60]. To estimate the weighted effect sizes across the studies we ran mixed intercept-only models, with lnRR as response variable and the paper ID as a random-effect factor to reduce collinearities between data extracted from the same study. The weighted effect sizes were reported as percent of changes [45] (Fig 2).

Overall, we calculated weighted effect sizes for parameters that were measured in at least three studies (Fig 2). In winter alpine soils, we revealed a significant decrease in water content (8.04%, $p<0.001$) and mean soil temperature (0.6˚C decrease, $p<0.001$) in snow removal experimental plots. During snowmelt period we demonstrated increase in microbial nitrogen content (51.52%, $p = 0.022$) and decrease in phosphatase activity (19.64%, $P = 0.014$) as well as presence of fungal PFLA (15.35%, $p<0.001$). Among bacteria, only Firmicutes demonstrated significant change in relative abundance at phylum level (2.48% increase in growing period, $p = 0.0016$). What is more, no significant effect on bacterial alpha-diversity was detected.

To estimate ecosystem-specific effects we focused on alpine forests in winter and during the snowmelt period due to limited number of measurements available for alpine grasslands and inconsistency in measured parameters between studies (S1 Table). We revealed significant decrease in soil water content in winter (9.47%, $p<0.001$) whereas during snowmelt period increase was demonstrated in DON (68.96%, $p = 0.007$) and nitrate content (36.7%, $p<0.001$). At the same time, no significant effects were demonstrated for ammonium content and urease activity neither in winter nor during snowmelt period in alpine forest soils (Fig 3).

4. Microbial activity and nutrient cycling

Seasonal snowpack affects soil biogeochemical state through changes in soil physical properties and input of water and nutrients during the snowmelt events [45]. However, it is difficult to develop a unified model of snow cover reduction effects on soil biogeochemical processes, as there are limited number of studies spanning different ecosystem types with inconsistent variables measured (nutrient levels, vegetation, and microbial community composition).

In general, insulation of soil via seasonal snowpack leads to an increased stabilization of soil temperatures facilitating microbial activity and respiration in winter soils [2,61]. Microbial biomass can even reach its annual peak values under the snowpack during winter [2,61]. More severe freezing of soils and an increased number of freeze-thaw events (under decreased snowpack) has a negative effect on microbial biomass and leads to the release of DOC and DON

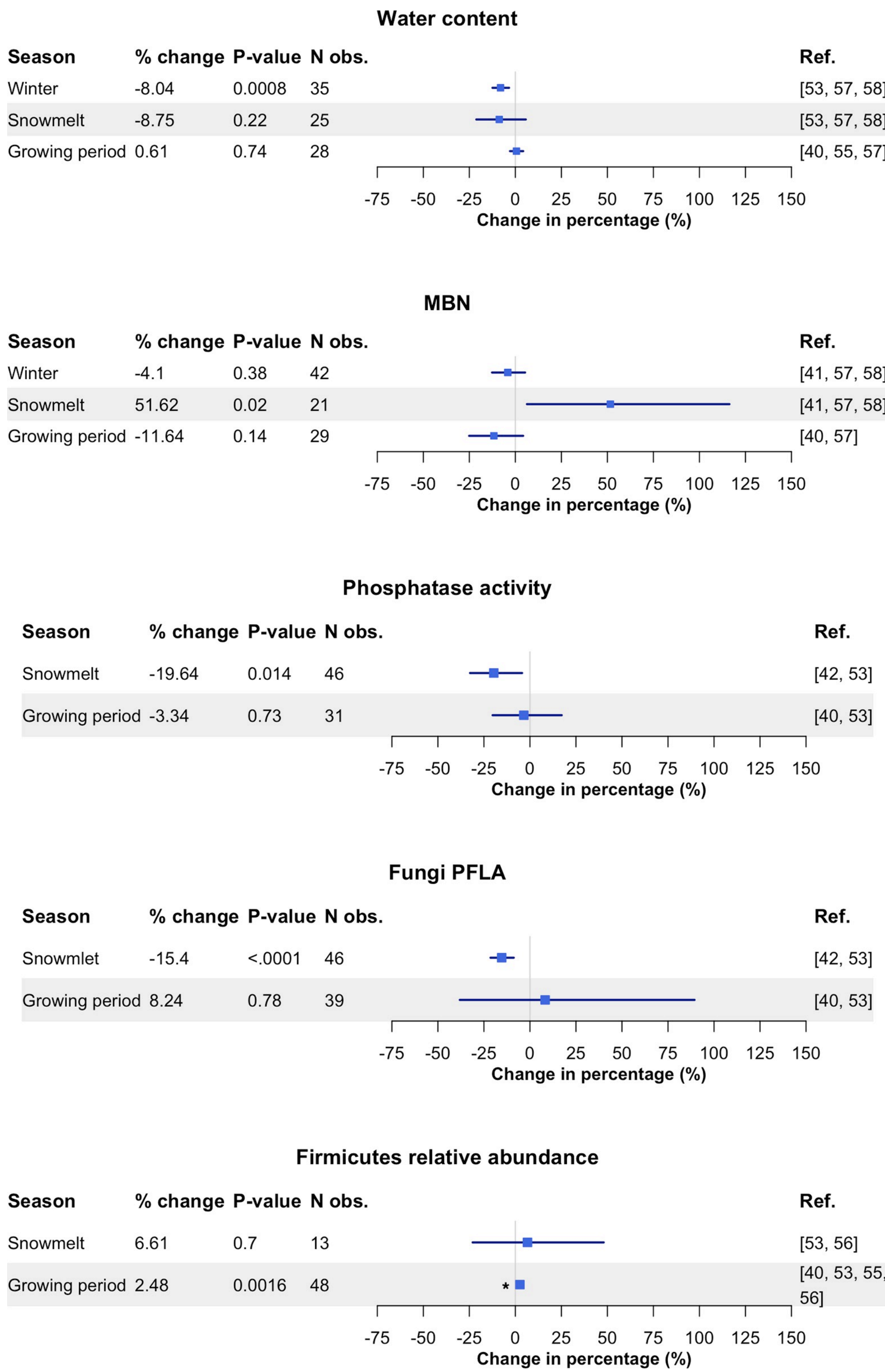

Fig 2. Effect of snow cover reduction on biochemical properties of alpine soils in snow removal experiments. Effects shown as percent of change with 95% confidence intervals. N obs.–number of observations, Ref.–data source references, MBN–microbial nitrogen, * - 95% confidence interval of [0.93%, 4.05%].

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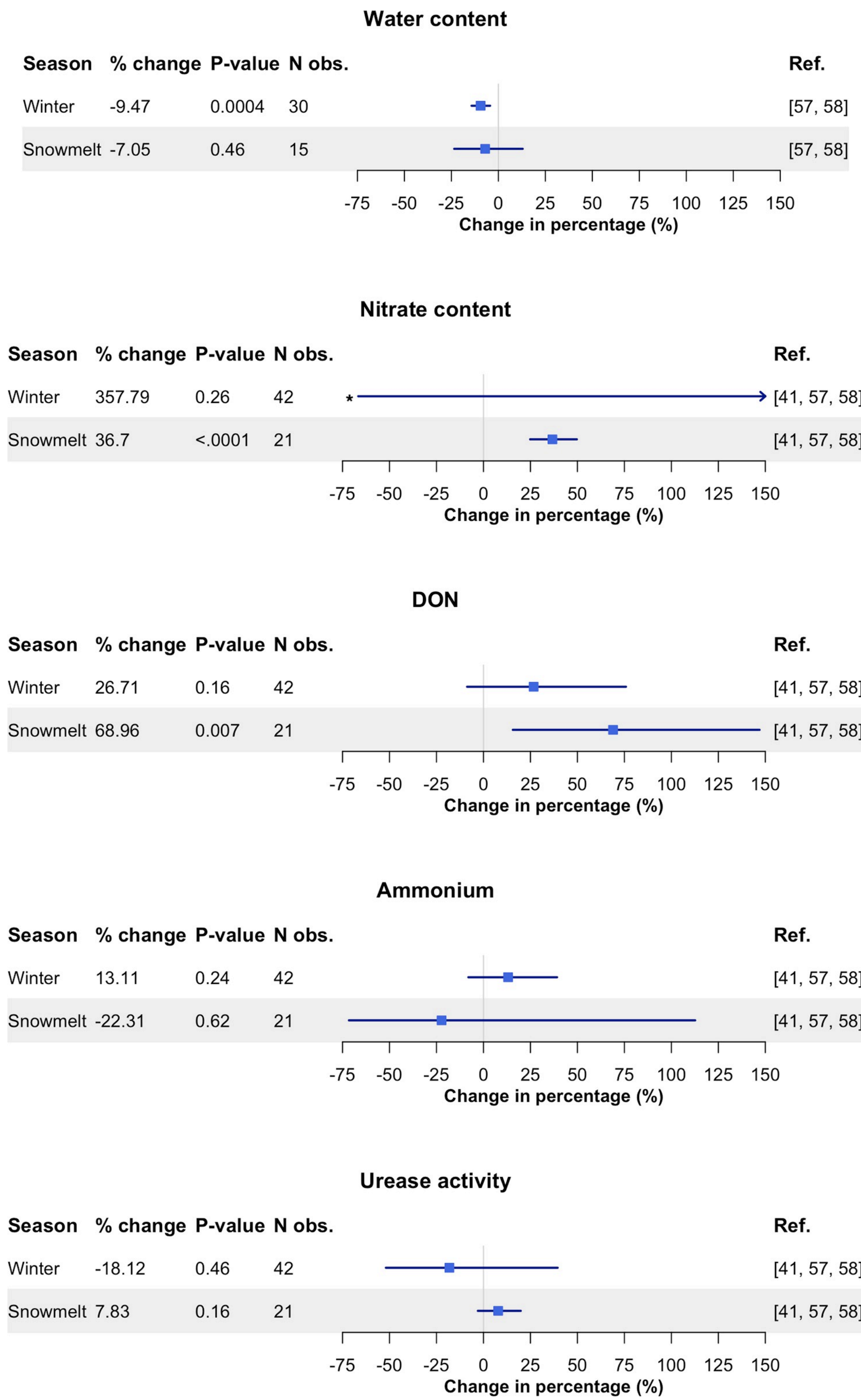

Fig 3. Effect of snow cover reduction on biochemical properties of soils in alpine forests in snow removal experiments. Effects shown as percent of change with 95% confidence intervals. N obs.–number of observations, Ref.–data source references, DON–dissolves organic nitrogen, * - 95% confidence interval of [-66.65%, 6184,74%].

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[62,63]. For example, microbial biomass carbon decreased in response to an increase of freeze-thaw cycles, which was also linked to reduced abundance of fungi in the community [64]. A similar decrease of microbial C (and decrease in microbial C:N) was demonstrated by Freppaz et al. (2008) for subalpine soils under reduced snow cover [46]. A more complicated dynamic in microbial biomass was revealed by Tan et al. (2014) in snow removal experiments, performed in the Tibetan Plateau alpine forest. The study demonstrated an initial decrease in microbial (C and N) biomass (16.92% and 52.91% decrease respectively) followed by an increase in microbial biomass later in the winter (32.88% increase in MBN) and during snowmelt period (66.21% increase MBC and 102.99% increase in MBN) in snow removed plots [57]; these results were corroborated by a separate Tibetan alpine forest study [41]. This late-winter increase in biomass may be explained by the increased activity of survived microorganisms which are stimulated by the input of nutrients from lysed cells [65,66]. As microbial biomass can act as a nitrogen sink in alpine catchments, loss of biomass from increased mortality due to increased freeze thaw cycles, could lead to higher nitrogen deposition to streams and downstream lakes during snowmelt period [67,68].

The activity of microorganisms in winter soils can be traced by measuring soil respiration levels [69]. Winter soil respiration under the snowpack was demonstrated in various ecosystems, including boreal and alpine forests [70,71], arctic and alpine tundra [72,73], and agricultural fields [74]. In alpine forests, respiration rates remain high during the winter and may contribute to the loss of up 50% of C assimilated by photosynthesis in the preceding growing season [71,75]. Therefore, with snowpack reduction, microbial activity and respiration may be expected to decrease. This pattern was demonstrated for alpine forest ecosystems in a snow manipulation experiment performed in the Tibetan Plateau [76] and long-term observations in the Rocky Mountains [77]. This results in a decrease of CO_2 emission during winter, leading to enhancement of carbon sequestration in forest ecosystems [71,78]. However, this is not always consistent, as no effect on winter soil CO_2 efflux rates was detected in snow removal experiments performed in subalpine grassland [36] and boreal forest [79].

Another proxy for microbial activity and cycling of carbon (C) and nitrogen (N) in soils under snowpack is evidence of extracellular enzymatic activity [80]. The activity of urease and invertase in soils are often used to infer microbial C and N cycling dynamics in biogeochemical studies [80]. Urease catalyzes the hydrolysis of urea (an organic N substrate) into NH_4^+, thus urease activity can be used as an index of N mineralization rate in soils [80,81], while carbon cycling can be accessed via invertase activity–an enzyme, that catalyzes the hydrolysis of sucrose to monosaccharides [82]. Tan et al (2014) demonstrated that reduction in snow cover resulted in decreased soil activity of both urease (56.94% decrease) and invertase (32.24% decrease) [57]. Similarly, Sorensen et al. (2016) demonstrated reduced overall enzymatic activity in mixed-hardwood forest soils as a result of an increase in soil frost formation [83]. A similar decrease in soil enzymatic activity during winter as a result of snow removal was reported in the alpine forest in the Tibetan Plateau and subalpine grassland in the European Alps [41,53,57,76]. During snowmelt period, we estimated 19.64% ($p = 0.014$) decrease in phosphatase activity in alpine soils in response snow cover removal (See 3. Snow manipulation experiments). The decrease in enzymatic activity may be associated with a reduction in net nitrification and N mineralization as was demonstrated in snow removal experiments in forest and subalpine grassland ecosystems [36,63,84]. However, Li et al. (2017) demonstrated an increase in N mineralization rate and N availability in snow removal plots in subalpine forest [41], while snow cover reduction and an increase in the number of freeze-thaw cycles led to increased ammonification rates in forests [41,58,85].

5. Microbial community structure

In ecosystems exhibiting strong seasonality, soil microbial community composition undergoes seasonal turnover [86]. For example, strong seasonal dynamics in soil microbial community structure was demonstrated for an alpine grassland and arctic tundra where high biomass winter communities were fungi-dominated, while lower biomass summer communities where bacteria-dominated [86–88]. The transition to summer communities can be abrupt during the snowmelt, as this period is marked by changes in soil temperature and shifts in liquid water availability and nutrients, as these environmental conditions favor the rapid propagation of bacteria [55,89]. With snow cover reduction, this transition is expected to happen earlier in the season, which can potentially disrupt seasonal nutrient exchange between soil microbiome and plants [90]. The snowmelt period is also associated with the exposure of soils to increased free-thaw cycles leading to microbial cells lysis, this provides an additional pulse of nutrients in the snowmelt period and potential shifts in microbial community composition [65,66].

In boreal forests, soil microbial community is dominated by frost-resistant taxa, such as Acidobacteria, insensitive to intensified freeze-thaw cycles [91,92]. In these communities, the winter-to-spring transition may have a reduced effect on bacterial and fungal composition [92]. However, this is not universal, as Gavazov et al. (2017) demonstrated that in European subalpine grasslands both winter and summer communities were dominated by bacteria, with a higher proportion of Gram-positive bacteria in winter compared to summer [36], incidentally, this study demonstrated no effect of snow removal on microbial community composition [36]. Isobe et al. (2022) demonstrated a declined richness of soil microbial community, but an increased abundance of Acidobacteria, Proteobacteria, Verrumicrobia, Planctomycetes and Actinobacteria in response to snow removal in cool-temperate forests (Japan), though this effect was diminished in growing season [93]. In contrast, in alpine ecosystems we reveled the increase in relative abundance of Firmicutes in growing period soils in response to snow removal (See 3. Snow manipulation experiment). In the Tibetan alpine forest, snow removal led to an increase in alpha-diversity during the late winter period. However, this had no legacy effect on the same soil community during the growing season [56]. Similarly, in a temperate North American forest, while there were initial differences in winter soil community composition between snow removal and control plots, revealed with PLFA fingerprinting, these differences were diminished by spring [94]. In general, the influence of snow cover reduction on soil microbial community composition has been rarely addressed and was assessed mostly with low taxonomic resolution techniques such as PLFA analysis [36,94], however as PLFA analysis is quantitative it can be used as a proxy of biomass of each microbial group [95]. The combination of 16S/18S/ITS rRNA amplicon sequencing with PLFA analysis can provide deeper understanding of microbial community structure allowing both higher taxonomic resolution along with quantification of biomass [40]. The application of metatransriptomics or metaproteomics can be used to assess physiological state and functional activity of the soil microbiome and its response to changes in snow cover regime.

6. Snowpack microbiome

Snow serves as an interface between the ground and the atmosphere, accumulating dust, microorganisms and other biological particles on its surface. Microorganisms are deposited on the snow surface via aerial transport of aerosol particles and precipitation [96]. The microorganisms can originate both from local sources [97] and from transport over long distances [98–101], depending on seasonal and meteorological conditions [102]. The origin of microorganisms in the atmosphere varies greatly with geography and may include different aquatic, terrestrial, animal, and plant surface sources [102].

Snow microbiome could act as a source of microbial species for colonization of underlying soils following the snowmelt [103,104], but more so because rapid seasonal shift during snow melt could constitute as an ecosystem disturbance which can favor colonization by new species [103,104]. This colonization potential of snow microorganisms was assessed by Mallard *et al*. (2022, 2023) in Arctic soils, where taxa originally unique to the snow medium were able to persist and establish in the soils following snowmelt [105,106]. Finally, since the snow microbiomes undergo post-deposition selection, favoring psychrotrophic stress-resistant microorganisms [107], future snow cover reduction/duration may result in reduced colonization of frost resistant microorganisms into the soils. This can then have a compounding negative effect on the biomass due to higher frost-induced mortality in soil microbes over time (speculative).

7. Plant root mortality

With the reduction of winter snow cover, plants are more exposed to freeze-thaw events that can lead to plant root damage and mortality followed by compensatory root regrowth in spring [108]. Fine root mortality leads to the release of organic matter that results in higher rates of soil N mineralization and inorganic N soil losses [109,110]. Such an effect was demonstrated in northern forests, where an increased number of freeze-thaw events led to root damage, increased soil ammonium in the early growing season, and reduction in root nitrogen uptake capacity [111]. Snow cover reduction also results in alternate snowmelt timing and reduced runoff volume [112], which has a downstream impact on plant phenology and plant growth rates during the snowmelt period [49,113,114]. For example, Bokhorst er al. (2008), demonstrated that mid-winter snow loss resulted in delayed bud development and reduced flower production of *Vaccinium myrtillus* L. [115]. Compounding this, reduced snow cover leads to drier soils in spring and summer resulting in potential water limitation in plants during the late growing season [26,43,116].

8. Soil fauna

The effect of snow cover reduction on soil-inhabiting fauna is not as widely studied as its influence on plants and microorganisms [117]. For terrestrial arthropods, winter snow-insulating properties are vital as a large proportion of arthropods hibernate in soil overlayed by snow [118]. Therefore, increased soil frost formation as well as the number of freeze-thaw events may lead to temperature-related arthropod injury and mortality [119,120]. For example, in snow-removal in the northern North American hardwood forest reduced arthropod richness and diversity during the growing season due to increased frost [121]. The microarthropod species richness as well as the population of enchytraeids (earthworms) was reduced in response to snow removal in pine forests, Finland [122]. Furthermore, this decline in soil-inhabiting fauna also has a direct impact on the biogeochemical soil cycles as meso- and microfauna contribute to via litter decomposition [123], and as the act as both decomposers of organic matter and grazers of bacteria and fungi [124].

9. Synthesis and future perspectives

With climate change, seasonal snow cover experiences a general negative trend in its depth, duration, and extent, which has a downstream effect on ecosystems (Fig 1) [2] (though climate change has uneven influence and may lead to a local increase in snowpack [12]). Though, snowpack reduction diminishes the insulating properties of snow, leading to a decrease in soil temperature, increased frost formation and freeze-thaw events. However, these effects can be diminished by the continual increase in air temperatures, which may lead to a decrease in the extent of seasonally frozen soil and higher soil temperatures [9,125]. The prevailing effect will rely on the degree of climate change and vary between ecosystems depending on multiple factors including their geographical location and local microclimate.

Changes in the physical properties of soil affect soil-inhabiting organisms including bacteria, fungi, plants, and animals. These effects may comprise of a decrease in microbial biomass and activity, microbiome composition changes, and increase in the mortality of plant roots and soil fauna [45,122,126]. This, in turn, is reflected in changes in soil geochemical cycles in winter and during the growing season [45]. However, these negative effects were not consistent across experimental studies, which may be partially explained by the adaptation of the soil inhabitants [91,92,118]. As soil biogeochemical interactions are complex and vary between ecosystems, it is hard to reveal a general pattern of soil response to snow cover reduction [36,92,93]. This is further complicated by the overall limited number of studies and the inconsistency of methodologies [46,52,55]. In this review, we synthesized data available for high-altitude ecosystems: alpine grasslands and alpine forests. In snow cover removal experiments, snow cover reduction had several general effects on alpine soils including decrease in water content and soil mean temperatures in winter that align with global meta-analysis performed by Zhao et al. (2022) [45]. At the same time, we identified increase in microbial nitrogen during snowmelt period and decrease in phosphatase activity. In addition, in alpine forests the snow cover removal affected nitrogen in soil during snowmelt period as the increase in nitrate and dissolved organic nitrogen was observed. These increase in DON and nitrate content in alpine forests soils during snowmelt may promote microbial activity in soils but also lead to loss of nutrients in early spring.

Snowpack reduction also has an indirect effect on soil microbiomes via reduced colonization potential of frost-resistant taxa from snow to soils, however, there are no studies assessing this potential effect. In general, in-depth winter soil community characterization has been performed in a limited number of studies, with only a few assessing the impact of snowpack reduction on soil microbiome composition and functioning [125]. The potential shifts in microbiome function may be addressed in future with the utilization of modern approaches (metatranscriptomics and metaproteomics). These studies would allow to acquire a complex view on the processes underlying alterations in geochemical cycles and, in broad, adaptation of soil microbiome to changing environments. Moreover, winter and the following growing season communities are rarely examined alongside in the same experiment. Often studies focus on the effect of snow cover removal over short periods which do not span across the winter, spring melt, and growing seasons. A systematic and multi-year monitoring of soil microbial communities under varied snow cover regimes could capture shifts and bigger trends in soil microbiome dynamics in response to climate change and subsequent snow cover reduction.

Supporting information

S1 Table. Data extracted from snow removal studies performed in high-altitude ecosystems. List of used abbreviations: Exp–data for snow removal plots, contr–corresponding control plots, SD–standard deviation; IN–inorganic nitrogen, TN–total nitrogen, DOC–dissolved organic carbon, DON–dissolved organic nitrogen, MBC–microbial carbon, MBN–microbial nitrogen, MBC_MBN–MBC:MBN ratio. Bacterial abundances are present as relative abundances.
(CSV)

Author Contributions

Conceptualization: Anastasiia Kosolapova, Ianina Altshuler.

Investigation: Anastasiia Kosolapova, Ianina Altshuler.

Writing – original draft: Anastasiia Kosolapova.

Writing – review & editing: Anastasiia Kosolapova, Ianina Altshuler.

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