



Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Impacts of snow-farming on alpine soil and vegetation: A case study from the Swiss Alps

Alexandre Buttler^{a,b,*}, Roland Teuscher^c, Nicolas Deschamps^a, Konstantin Gavazov^b, Luca Bragazza^d, Pierre Mariotte^{a,b,e}, Rodolphe Schlaepfer^a, Vincent E.J. Jassey^{a,b,f}, Lucas Freund^{a,d}, Jessica Cuartero^g, Juan Carlos Quezada^{a,d,h}, Beat Frey^g

^a School of Architecture, Civil and Environmental Engineering (ENAC), Ecole Polytechnique Fédérale de Lausanne (EPFL), Station 2, 1015 Lausanne, Switzerland

^b Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Site Lausanne, Station 2, 1015 Lausanne, Switzerland

^c Ob. Bahnhofstrasse 22, 3714 Frutigen, Switzerland

^d Agroscope, Field-Crop Systems and Plant Nutrition, Route de Duillier 50, P.O. Box 1012, CH-1260 Nyon, Switzerland

^e Agroscope, Grazing Systems Group, 1725 Posieux, Switzerland

^f Laboratoire Ecologie Fonctionnelle et Environnement, Université Paul Sabatier, CNRS, 31062 Toulouse Cedex, France

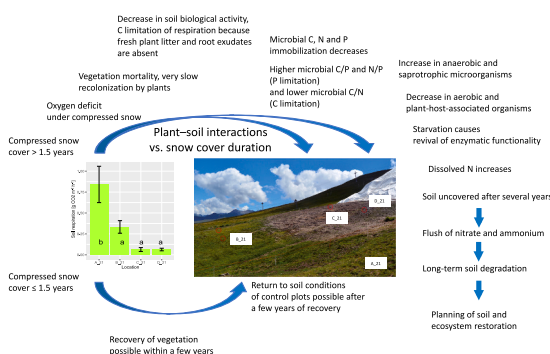
^g Swiss Federal Institute for Forest, Snow and Landscape Research WSL, 8903 Birmensdorf, Switzerland

^h Asian School of Environment, Nanyang Technological University, 50 Nanyang Avenue, Singapore 639798, Singapore

HIGHLIGHTS

- Beyond 1.5 years of compressed snow cover, plant mortality was high and few species recolonized the soil.
- Soil biological activity decreased drastically and persistently under prolonged compressed snow cover.
- Microbial C, N and P immobilization decreased under compressed snow cover.
- Microbial C/N decreased after longer compressed snow cover and subsequent recovery.
- Anaerobic and saprotrophic microorganisms were favored under compressed snow cover.

GRAPHICAL ABSTRACT



ARTICLE INFO

Editor: Charlotte Poschenrieder

Keywords:

Ski resort

Snow pile

Carbon

Nitrogen

Anaerobic microorganism

Saprotrophic microorganism

ABSTRACT

Snow-farming is one of the adaptive strategies used to face the snow deficit in ski resorts. We studied the impact of a shifting snow-farming technique on a pasture slope in Adelboden, Switzerland. Specifically, we compared plots covered by a compressed snow pile for 1.5, 2.5 or 3.5 years, which then recovered from the snow cover for three, two or one vegetation seasons, respectively, with control plots situated around the snow pile.

In plots with >1.5 years of compressed snow pile, plant mortality was high, recovery of vegetation was very slow, and few plant species recolonized the bare surface. Soil biological activity decreased persistently under prolonged snow cover, as indicated by reduced soil respiration. The prolonged absence of fresh plant litter and

* Corresponding author at: School of Architecture, Civil and Environmental Engineering (ENAC), Ecole Polytechnique Fédérale de Lausanne (EPFL), Station 2, 1015 Lausanne, Switzerland.

E-mail address: alexandre.buttler@epfl.ch (A. Buttler).

<https://doi.org/10.1016/j.scitotenv.2023.166225>

Received 24 April 2023; Received in revised form 8 August 2023; Accepted 9 August 2023

Available online 14 August 2023

0048-9697/© 2023 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

root exudates led to carbon (C) limitation for soil microbial respiration, which resulted in a significant decrease in the ratio of total organic carbon to total nitrogen (TOC/TN) under the snow pile.

Microbial C, nitrogen (N) and phosphorus (P) immobilization decreased, while dissolved N concentration increased with compressed snow cover. Longer snow cover and a subsequent shorter recovery period led to higher microbial C/P and N/P but lower microbial C/N. Nitrate and ammonium were released massively once the biological activity resumed after snow clearance and soil aeration.

The soil microbial community composition persistently shifted towards oxygen-limited microbes with prolonged compressed snow cover. This shift reflected declines in the abundance of sensitive microorganisms, such as plant-associated symbionts, due to plant mortality or root die-off. In parallel, resistant taxa that benefit from environmental changes increased, including facultative anaerobic bacteria (Bacteroidota, Chloroflexota), obligate anaerobes (Euryarchaeota), and saprophytic plant degraders.

We recommend keeping snow piles in the same spot year after year to minimize the area of the impacted soil surface and plan from the beginning soil and ecosystem restoration measures.

1. Introduction

The general decrease in snow depth and snow cover duration since the end of the 1980s throughout the European Alps poses a great challenge for winter tourism in ski resorts at low and medium altitudes, and the winter tourism industry has already begun to respond to the implications of these changes (König, 1999; Abegg, 2011; Marty, 2013). Current technical solutions, such as snow-making, grooming and snow-farming (the storage and conservation of snow, generally during the warm season of the year, for use in the subsequent winter season), are adaptive strategies to face this snow deficit, but they have their limitations.

While studies on snow-farming *per se* are rare, there are more studies on artificial snow, snow grooming and compression, and the associated effects on soil and vegetation development (Kammer, 2002; Keller et al., 2004; Rixen et al., 2008; Zeidler et al., 2008, 2014; Steinbauer et al., 2018; Bacchiocchi et al., 2019). For example, Newesely et al. (1994) demonstrated that compressed snow can seriously damage plants. Furthermore, the physico-chemical properties of soil under groomed ski runs have been reported to differ from those of soil under natural snow deposits (Allegrrezza et al., 2017).

Snow-farming emerged in Scandinavia more than a decade ago as a technique to conserve snow for touristic purposes, and it is now also applied in the Alpine regions. It allows ski resorts to be less dependent on weather conditions and helps them to secure important sports events with the preparation of adequate runs. Such events are, for example, the Cross-Country World Cup in Davos, Switzerland, where it was introduced successfully in 2008 already, the Biathlon World Cup in Östersund, Sweden, and the Ski Jumping World Cup in Titisee-Neustadt, Germany. The largest application of snow storage was performed for the Winter Olympics held in Sotschi (Russia) in 2014, where about 800,000 m³ of snow was amassed as a reserve for the preparation of alpine ski-racing courses in case of a lack of snow (Lintzen, 2016 in: Grünewald et al., 2018). In snow-farming, the stored snow results either from artificial snow produced with snow-making machines for this purpose, which is feasible only under low temperatures, or from the collection of natural snow at the end of the winter. The snow is then insulated using organic (e.g. sawdust, chipped wood, cutter shavings, bark mulch, or straw) or synthetic materials (e.g. polystyrene plates, polymeric foam, or geotextiles) (Skogsberg and Lundberg, 2005). All these materials act as insulating layers that reduce heat transfer from the atmosphere to the snow (Grünewald et al., 2018). In Adelboden, Switzerland, where the present study was conducted, snow is farmed on a pasture slope, by accumulating natural snow at the end of the winter, for use on a downhill ski run. This application is in contrast to the snow-farming in Davos, where the snow is machine-made and accumulated on a flat gravel area, to be used for preparing a cross-country ski course. In Adelboden, the rationale is early ski course preparation, generally in mid-October, before winter snowfall begins. The prepared course is then rented out to ski teams for training.

Seasonal snow cover provides a unique soil environment capable of

supporting high levels of biogeochemical activity, which significantly impacts annual carbon and nutrient cycles (Brooks et al., 2011). When snow is repeatedly accumulated artificially on a living soil, and covers the soil for one to several years, various impacts underneath the snow pile can be expected. As the literature on snow-farming is scarce, we refer to published work in winter ecology, in particular snow manipulation experiments and studies on the effects of climate change on snow deposits. We expect parallel mechanisms to apply after a prolonged (*i.e.* several years) compressed snow accumulation (see reviews by Wipf and Rixen, 2010; Rixen et al., 2022, Zhao et al., 2022). Specifically, this literature suggests that snow-farming could lead to: (i) a deficit in the transfer of photosynthetic assimilates to the soil (Kappen, 1993; Hui et al., 2018); (ii) changes in soil physical properties (temperature, moisture, gas exchange; Brooks et al., 2004); (iii) changes in soil biota (e.g. microbial activity; Sorensen et al., 2019); and (iv) changes in nutrient availability and cycling (Brooks et al., 2011; Freppaz et al., 2007a; Kuhn, 2001). Furthermore, in the run-off zone below the accumulated snow on a slope, additional impacts could include: (v) a change in the duration of the vegetation period under the influence of cold water from the melting snow; (vi) a change in plant species composition, diversity and phenology; and (vii) increased soil erosion (Hudek et al., 2020).

In a case study of the snow-farming application in Adelboden, we conceived a shifting snow-farming design, where the exact position of the snow pile was changed each year over three years. We expected this practice to be less harmful to the living pasture soil and to support its recovery. Specifically, we (i) compared soils covered with a snow pile of several meters depth for several years with control soils not affected by summer snow storage, and (ii) investigated the effects of the duration of the compressed snow cover and of the recovery period after the cover.

We hypothesized that (i) vegetation recovery would be slow when the compressed snow accumulated for several years, and only a few species would recover and become dominant; (ii) prolonged low temperature and oxygen deficit under the compressed snow would decrease soil biological activity; (iii) microbial carbon (C), nitrogen (N) and phosphorus (P) immobilization would decrease under compressed snow; (iv) anoxic conditions would slow C turnover, and this translates to increased concentrations of soil dissolved organic carbon (DOC); (v) several years of compressed snow cover would shift the soil microbiome towards oxygen-limited prokaryotic taxa and saprophytic fungi; and (vi) once the soil was cleared from snow and aeration resumed, the revival of biological activity would be marked by a flush of N.

2. Material and methods

2.1. Field site and snow conservation

The snow-farming experiment was installed on Tschentenalp Schwandfeld, a former World Cup ski slope, at 1600–1960 m a.s.l. (46°30'5"N, 7°32'39"E), above and northwest of the ski resort of Adelboden. The city of Adelboden is well known for the annual World Cup, which now takes place every January on the Chuenis ski slope (Suppl.

S1). The Tschentalp slope is on a north-facing natural (ungraded) alpine pasture characterized by *Nardus stricta* (matgrass), which is grazed by cows from the end of June to the end of August for local hard-cheese (slab cheese) production. The pasture covers a total surface of 158 ha (mostly open pastures, but also some pasture woodlands and hay meadows), and is managed by a local pasture consortium. The soil is generally deep, acidic, and wet in some parts, with few rocky outcrops and a low limestone content. It lies mostly on slate pads (Dystric-Cambisols, Gleyic-Cambisol; IUSS Working Group WRB, 2015). The site is generally covered with natural snow for 6 months each year.

In winter 2017–2018, the local ski training center started to accumulate natural snow on this slope to create a training run next to one of the ski lifts in mid-October, before the snow starts to fall in winter. In doing so, they can offer an early training option in the region. In April 2018, the local government provisionally authorized the ski center to run the snow-farming for a trial period of 5 years. A scientific impact study was required, and a final report was delivered in November 2021 (Teuscher and Buttler, 2021), which stressed the need for adaptive management and included some recommendations for limiting the ecological impact of the snow-farming.

Snow is accumulated in April of each year with a snowcat, a fully tracked vehicle designed to move on snow. The snowcat forms a snow pile of about 100 m long, 40 m wide, and 6 m tall, halfway along one of the ski lifts (Suppl. S2). The snow is then covered with insulating expanded polystyrene (EPS) plates (swisspor AG, Steinhausen, Switzerland) and a white geotextile sheet. In mid-October, the cover sheet is removed and stacked in the vicinity, and the ski slope is prepared with a snowcat using the accumulated snow so that the ski training can start shortly thereafter. Snow is compressed through its own weight and through the coming and going of the snowcat heavy machine when snow is accumulated in April, and when the snowpack is reworked for the ski run preparation in October. In the following winter, the snow pile is rebuilt and placed slightly higher along the slope.

2.2. Experimental design

Initial conditions could not be assessed during the 2017 vegetation

season. Instead, we started sampling the soil underneath the prepared ski run in October 2018 (after 1 year of snow cover). We established three plots at each of three positions along the snow pile (Fig. 1, plots 19–27). This sampling was done because we wanted to also have a short-term response of the soil properties, when the soil was still covered by the snow pile, thus without any period of recovery. Since the snow pile was shifted each year uphill of one third of its length, which is about 30 m every year for three years, plots that had been covered became accessible for monitoring in the following years (Fig. 1). These plots were covered with compressed snow for 1.5 years (location B, plots 25–27: first winter, following summer and second winter, up to snow-melt), 2.5 years (location C, plots 22–24), or 3.5 years (location D, plots 19–21), and then recovered (no compressed snow) for 3, 2, or 1 vegetation periods, respectively, until the end of the recording period in autumn 2021. We further set up reference plots in triplicate along the right and the left sides of the snow pile (locations A, $N = 6$, plots 7–9 and 16–18), where the environmental conditions (vegetation, soil, slope) were similar to those in the plots covered with compressed snow (Fig. 1). Finally, we established plots at the lower margin of the snow pile (location E) in the run-off area (Fig. 1; plots 10, 11 and 12 were in the wet run-off area; plots 13, 14 and 15 were in a dryer area). We set up plots 1 to 6 (not shown in Fig. 1) at the upper margin of the snow pile in 2018 to represent initial conditions, but they were covered with snow throughout the experiment and therefore could not be sampled. All plots were 2 m × 2 m in area; we marked their positions with two wooden poles driven to ground level and we georeferenced their positions with a GPS. Plots not covered with compressed snow could be grazed by roaming cattle during the vegetation period.

2.3. Vegetation survey

We surveyed the plots every year at the peak of biomass production, between mid-August and early September. The vegetation survey followed the frequency method (Daget and Poissonet, 1971), with 5 lines across the plot, each with 9 points where we recorded contacts with individual plants (45 points total). We recorded all plants, including mosses and lichens.

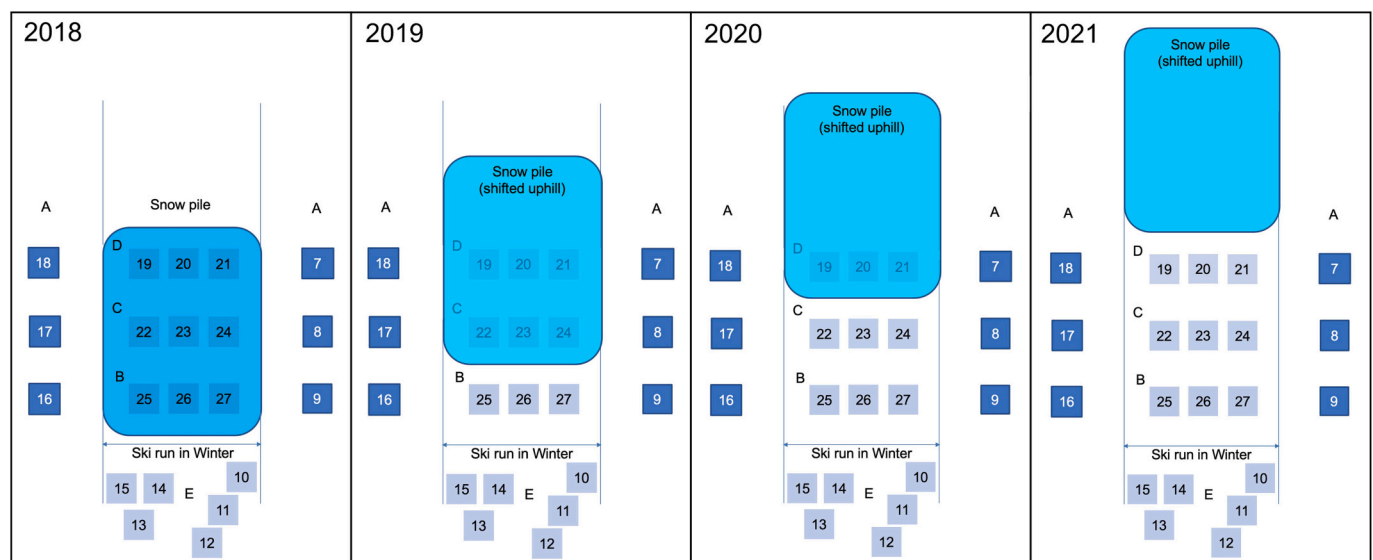


Fig. 1. Design of the snow-farming experiment. The snow pile of ca 25,000 m³ (i.e. 100 m × 40 m) was established on the pasture slope in April 2018. In the following years (2019, 2020 and 2021), it was shifted uphill by about one-third of its length along the slope, meaning that the lowest section was freed from snow the following spring. Different sections were therefore covered for 1.5, 2.5 or 3.5 years. Three plots were set up in each section of the snow pile: 1.5 years (location B), 2.5 (location C) and 3.5 years (location D). Reference plots were set up in triplicate on the right and left sides of the snow pile (locations A). Plots 10 to 15 (location E) were established in the run-off area at the lower margin of the snow pile (plots 10, 11 and 12 in the wet run-off area, plots 13, 14 and 15 in a drier area). Plots 1 to 6 (not illustrated) were set up at the upper margin of the snow pile in 2018 to represent initial conditions, but they were covered throughout the experiment and therefore could not be used to assess the vegetation and soil.

2.4. Soil sampling and field measurements

Soil sampling took place in 2018, 2020 and 2021. In 2018, we sampled the control plots in late September, while we sampled the plots lying underneath the compressed snow in mid-November, once the ski run was prepared, so that we could use a corer to drill through the snow layer. In the 2020 and 2021, we sampled both the control plots and the newly snow-free plots in early September. In each plot, we collected nine samples (only five in 2018, when sampling was done underneath the snow) of the topsoil, i.e. 0–10 cm depth, with a single gouge auger 3 cm in diameter (Royal Eijkelkamp, Giesbeek, the Netherlands). We then prepared a composite sample from each plot in the field, after removing stones and coarse debris larger than 2 mm in diameter. We stored the composite samples for a few days at 4 °C temperature until processing, and we deep-froze at –80 °C (to insure biological stability) two subsamples from the composite sample from each plot for enzymatic and microbial community measurements.

In the field, we measured soil respiration, temperature and moisture at three locations within the plots. First, we measured soil respiration (RS, g CO₂ m² h^{–1}) with a portable EGM-4 environmental gas analyzer (PP System, Amesbury, MA, USA) in spots where there was little vegetation, preferably on flat surfaces, but avoiding locations recently disturbed by cattle. We cut any plants present at ground level. Immediately after removing the respiration chamber, we measured soil temperature (T, °C; HI-98501 Checktemp digital thermometer with stainless steel penetration probe; Hanna Instruments, Woonsocket, RI, USA) and soil volumetric water content (VWC, %; FieldScout TDR 300 m with 12 cm rods; Spectrum Technologies, Inc., Aurora, IL, USA) in the topsoil (0–12 cm depth) in the same spots. We averaged these measurements at the plot level.

2.5. Soil biogeochemical analyses

In the laboratory, we determined soil pH in a 1:2.5 soil-to-water slurry. We additionally determined soil water content gravimetrically by drying soil subsamples at 100 °C to a constant weight, so that further analyses could be expressed in reference to dry soil. We analyzed total organic carbon (TOC) and total nitrogen (TN) contents in the bulk soil using fresh soil. We determined soil C and N concentrations (mg kg^{–1} dry soil) under high-temperature oxidation using an elemental analyzer (NA2500 Nitrogen Carbon Analyzer, CE Instruments, Hindley Green, UK). For the determination of microbial biomass C (Microbial C) and N (Microbial N), we weighed out two samples of approximately 5 g of fresh soil for each replicate. We immediately extracted one sample in 25 ml of a 0.5 M K₂SO₄ solution (Vance et al., 1987), whereas we put the other sample in a vacuum desiccator and subjected it to fumigation with chloroform vapor. After one day of fumigation, we extracted the fumigated soil samples with the same 0.5 M K₂SO₄ solution. We analyzed TOC and TN concentrations in the extracts of fumigated and non-fumigated samples using a TOC/TN analyzer (TOC-V; Shimadzu, Kyoto, Japan). We additionally analyzed soil water soluble organic C (DOC) and total dissolved N (TDN) with the TOC/TN analyzer. To determine the soil available phosphorus (P) and the microbial P (Microbial P), we extracted 3 g of fumigated and non-fumigated fresh soil with 40 ml NH₄F (P-Bray method). We analyzed the inorganic P content of the extracts by colorimetry using a spectrophotometer at 890 nm. We estimated microbial biomass C, N and P as the differences between the amounts of C, N and P after and before fumigation using an extractability factor of 0.45 for C (Vance et al., 1987), 0.54 for N (Brookes et al., 1985), and 0.4 for P (Brookes et al., 1982). Microbial biomass C, N and P and soil available P are expressed as mg kg^{–1} oven-dried soil. We determined ammonium (NH₄⁺) and nitrate (NO₃[–]) concentrations by continuous flow analyses using an automated analyzer (SEAL AA3 HR Autoanalyzer, Seal Analytical, Norderstedt, Germany) after extraction of 5 g of fresh soil with 30 ml of 1 M KCl, expressing values as mg kg^{–1} oven-dried soil. We then calculated ratios of TOC/TN, TOC/P, TN/P and

DOC/TDN.

We quantified the soil potential enzyme activities using a catabolic response profile approach by measuring the activities of five hydrolytic enzymes under saturating substrate conditions and stable temperature (25 °C), following a slightly modified fluorescence-based method (Marx et al., 2005). More specifically, we measured the activities of β-glucosidase (BG), β-xylosidase (BX), β-N-acetylglucosaminidase (NAG), leucine aminopeptidase (LAP) and acid phosphatase (AP). Briefly, we conducted assays in 96-well dark microplates, with three replicate wells per sample per assay. We mixed approximately 1 g of deep-frozen soil with 125 ml of phosphate buffer and stirred the mixture for 2 min on a magnetic stirrer. We then added 100 μl (200 μM) of appropriate 4-methylumbelliferone (MUB) or 7-amino-4-methylcoumarin (MUC) substrate to each well. We incubated the microplates in the dark at 22 °C for 0.5 h for AP and NAG, 2 h for BG and BX, and 24 h for LAP activities. At the end of the incubation times, we added 30 μl of 0.5 M NaOH to each well. We measured fluorescence using a microplate fluorometer with 365-nm excitation and 460-nm emission (BioTek Instruments, Winooski VT, USA). In parallel, we prepared a set of standards with 200 μl of soil slurry solution of each sample with a range of MUB or MUC standards concentrations (0, 2.5, 5, 10, 25 and 50 μM). We calculated enzyme activities from the regression parameters of the standard curve, along with the fluorescence mean values of the soil samples; these values are reported as μmol substrate (MUB or MUC) g^{–1} soil Cmic h^{–1}.

2.6. DNA extraction, amplicon sequencing, and bioinformatic processing

We extracted total DNA from 0.5 g of stored soil using the DNeasy PowerSoil Pro Kit (Qiagen, Hilden, Germany), and we quantified the DNA extracts with PicoGreen (Invitrogen, Carlsbad, CA, USA). To remove foreign DNA and prevent microbial contamination, we cleaned workbench surfaces and non-autoclavable materials with 5 % sodium hypochlorite and 70 % ethanol solutions prior to the DNA extractions. We performed triplicate PCR amplifications of the V3–V4 region of the 16S rRNA gene (prokaryotes) and of the ITS2 genomic region (fungi) on 40 ng of the extracted DNA samples, using the primer pairs 341F/806R and ITS3/ITS4 under the conditions described in Frey et al. (2016). We included negative controls for the DNA extractions (extraction buffer without soil) and PCR amplifications (high-purity water without DNA template). We then pooled and purified (AMPure XP beads; Beckman Coulter, Beverly, MA, USA) the amplicon triplicates and sent them to Microsynth (Balgach, Switzerland), where the pooled amplicons were paired-end sequenced using the Illumina MiSeq v3 platform (Illumina Inc., San Diego, CA, USA). Raw sequences were deposited in the NCBI Sequence Read Archive under the BioProject accession identifier PRJNA933548.

We carried out sequence analyses using the Quantitative Insights Into Microbial Ecology 2 program (QIIME 2, ver. 2020.6.0; Bolyen et al., 2019) run on the WSL Hyperion cluster. We imported the raw paired-end FASTQ files into the QIIME2 program and demultiplexed them using a native plugin. Thereafter, primer was trimmed using the Cutadapt. We used the Divisive Amplicon Denoising Algorithm 2 (DADA2) plugin in QIIME2 for quality filtering and for determining amplicon sequence variants (ASVs; Callahan et al., 2017). We trimmed and denoised the demultiplexed FASTQ file, removed the chimera, and merged the data (Callahan et al., 2016). We applied the parameter with a truncation length of 270 bp for forward and 215 bp for reverse (for bacteria) and of 240 bp for forward and 205 bp for reverse (for fungi). We accomplished taxonomic assignment using the Naive Bayes q2-feature-classifier (Bokulich et al., 2018) in QIIME2 against the SILVA ribosomal RNA gene database v138 (Quast et al., 2013) and the UNITE database v8.2 (Nilsson et al., 2019). We filtered out prokaryotic ASVs mapped to mitochondria and chloroplasts from the resulting prokaryotic feature table. We did not remove archaeal sequences, but we used the term “bacterial community/diversity” in the manuscript because bacterial taxa dominated the communities of all soil samples. We randomly

subsampling the FASTQ files to the smallest read number to enable a more accurate comparison of the richness of the different samples.

2.7. Statistical analyses

We carried out all statistical analyses in R v4.2.2 (R Core Team, 2022) through RStudio v2022.07.2. We analyzed soil biochemical variables by means of linear mixed-effects (LME) models (*nlme*, v.3.1), followed by analysis of variance (ANOVA) with type III sum-of-squares to account for the unbalanced design (*car*, v.3.1.1; Fox et al., 2019). First, we analyzed the data from 2021 separately, using location A (control plots), B (snow pile cover for 1.5 years and 3 vegetation seasons of recovery), C (snow pile cover for 2.5 years and 2 seasons of recovery), and D (snow pile cover for 3.5 years and 1 season of recovery) as fixed effects and plot as a random effect on the intercept. We also used LME models for the 2018 data, comparing the effect of 1 year of compressed snow cover in locations B, C and D with the control plots in A. Finally, we used three LME models with the entire data set of years 2018, 2019 and 2020 to determine individually the effects of the compressed snow cover (factor, categorical variable), the number of years under compressed snow cover (quantitative variable), and the number of vegetation seasons of recovery (quantitative variables), as well as their respective interactions with the year of sampling.

For each model, we checked model assumptions, focusing on the normality of residuals, using visual assessment of histogram plots and formal Shapiro-Wilks tests, and qqnorm plots. When model assumptions were not fulfilled, we log-transformed the data or used a permutation test with 'PermTest' function (*pgirmess*, v.2.0). We ran post-hoc multiple comparisons tests using 'glt' function (*multcomp*, v.1.4) and added letters to denote significant differences between categories in some figures.

We analyzed the vegetation surveys of 2018, 2019, 2020 and 2021 with a redundancy ordination analysis (RDA; *rda*, *vegan* v. 2.6). This method enabled an overall comparison of the plots with different snow cover durations and with different recovery durations, and could be used to test the explanatory variable (snow cover duration vs controls). We applied a Hellinger transformation to the vegetation frequency data and used a correlation matrix for the ordination. We additionally used RDA to give an overall view of the plots described by biogeochemical variables in 2018, 2020 and 2021, taking as explanatory variables the duration of compressed snow cover and the duration of recovery. We completed the same analysis with the data set from 2021, which made it possible to integrate the additional variables NO_3^- , NH_4^+ , and enzymatic activities. We log-transformed the data and used a correlation matrix for the ordination.

We analyzed microbial communities with the *microeco* package v. 0.13 (Liu et al., 2021). First, we performed technical filtering, removing singletons and spurious ASVs (mitochondrial and chloroplast sequences). We estimated microbial alpha-diversity (richness and Shannon index) on rarefied microbial data using the 'trans_alpha' function in *microeco*. To test the difference between the different locations, we assessed normality and homogeneity of variance using Shapiro-Wilk and Levene's tests using the 'car' package, following the assumptions and using the functions described by Cuartero et al. (2022). We performed principal coordinates analysis (PCoA) using the Bray-Curtis distance to visualize the variation in microbial community composition using the 'trans_beta' function in 'microeco'. To evaluate the effect of the location, we conducted a permutational multivariate analysis of variance (PERMANOVA) when the homogeneity of variance assumption was met. When homogeneity was not fulfilled, we used an analysis of similarities (ANOSIM) instead. To study the composition of the microbial communities, we used the 'trans_abund' function in 'microeco' to calculate the relative abundance at three different levels: phylum, order and genus. Relative abundance is represented in barplots. We used two different approaches to identify the most representative microorganisms for each location: linear discriminant analysis effect size (LEfSe; Segata et al., 2011) and analysis of compositions of microbiomes with bias correction

(ANCOMBC; Lin and Peddada, 2020). We performed LEfSe for all the taxa levels using the 'trans_diff' function in *microeco*. The LEfSe algorithm involved three steps: (i) a non-parametric Kruskal-Wallis test to detect statistical differences between abundances; (ii) a pairwise comparison test between subclasses using the Wilcoxon rank-sum test to evaluate the biological consistency; and (iii) a linear discriminant analysis (LDA) to estimate the effect size between abundances with default parameters (Cuartero et al., 2021). We performed the third step at the phylum, order and genus levels with the 'ancombc2' function in the ANCOMBC package v 2.0.2. This algorithm estimates the unknown sampling fractions, corrects the bias induced by their differences through a log-linear regression model, and identifies taxa that are differentially abundant according to the location. We generated all visual representations of the data and analyses using the *ggplot2* package v3.4.0.

3. Results

3.1. Response of vegetation to compressed snow cover

On average during the period 2018 to 2021, we observed 18 plant species in the 3 control plots on the right side of the snow pile (plots 7, 8 and 9), and 19 plant species on the left side of the snow pile (plots 16, 17 and 18). These numbers are much larger than those in plots covered by the snow pile. In the plots that were covered for 1.5 years (plots 25, 26 and 27), we recorded five to seven plants species after 1 year of recovery (2019), three to four after 2 years of recovery (2020), and four to five after 3 years of recovery (2021). In the plots that were covered for 2.5 years (plots 22, 23, and 24), we detected no species in the first year (2020), and four to five in the second year (2021). In the plots that were covered for 3.5 years, we recorded only one or two species in the first vegetation season (2021). The map of plant species richness (Suppl. S3) and the photos of the plots (Fig. 2) illustrate the slow recovery in the plots that had been covered by the snow pile. A scatter plot of the RDA (Fig. 3) shows that only a few species contributed to the recovery: *Juncus filiformis*, *Nardus stricta*, *Viola biflora* and *Carex nigra*. Interestingly, *Nardus stricta*, which was always well represented in the control plots, hardly recovered when the compressed snow cover was present for >1.5 years. In contrast, *Juncus filiformis*, which was not constantly represented in the control plots, reached high constancy in the first year of recovery in plots covered for only 1.5 years. While most of the control plots lie on the opposite side of the scatter plot relative to the plots in the snow pile, the three control plots in the wet zone (plots 10, 11 and 12) had a very different species composition relative to the other control plot and to the plots in the snow pile.

3.2. Response of soil to compressed snow cover

An overall picture of biogeochemical parameters, comparing control plots in locations A (plots 7 to 9 and 16 to 18) and E (13 to 15) with plots that were covered with the snow pile in locations B, C, and D (19 to 27), is given in the scatter plot of the RDA, which includes years 2018, 2020 and 2021 (Fig. 4). Soil samples collected underneath the snow pile in 2018 showed, already after 1 year, a deficit of extractable P relative to TOC and TN (TOC/P, TN/P), as well as high concentrations of TN (see also Table 2 and suppl. S7). There was also a significant decrease in TOC/TN after 1 year of compressed snow cover (Suppl. S7). After longer durations of compressed snow cover (1.5, 2.5 and 3.5 years) and subsequent recovery (1, 2 or 3 seasons), this deficit of P relative to C and N appeared in the microbial biomass (microbial C/P and N/P), and in TDN (Fig. 4 and Suppl. S5). These patterns contrast with that in the control plots, which had high values for microbial biomass C, N and P. Control plots were also characterized by high microbial biomass C/N and high TOC/TN, and to some extent also high DOC/TDN, indicating a N deficit. The stoichiometric ratios given in Fig. 5 (see Suppl. S8 and S9 for other variables and their statistical significance) indicate a rather rapid



Fig. 2. Top: Photo taken in July 2020 of the snow pile's impact on soil and vegetation after prolonged compressed snow cover. Yellow circles indicate surfaces that had been covered for 1.5 years (on the left) and for 2.5 years (on the right). Bottom: Photos of individual plots, taken in August 2021. Plots 16, 17 and 18 belong to the control plots, and plots 27, 24 and 21 had been covered with compressed snow for 1.5 years (3 seasons of recovery), 2.5 years (2 seasons of recovery), and 3.5 years (1 season of recovery), respectively.



recovery for TOC/P and TN/P, while microbial biomass C/P and N/P only increased again after 1 or 2 years of recovery.

Taken separately, data from year 2021 can be used to assess in more details the combined effect of compressed snow cover duration and duration of recovery in the following vegetation seasons (Table 1 and Suppl. S4 and S5). Here, soil temperature was clearly reduced by the compressed snow cover and differed significantly between locations A, B, C and D, due to the influence of the run-off of cold water from the snow pile. On the other hand, soil respiration was significantly lower than in control plots in all locations that had been covered by compressed snow but did not differ significantly between locations B, C and D. NH_4^+ concentrations were significantly higher in location D than in the other locations, indicating a flush of N after 3.5 years of snow cover. In location C, where the soil was in the second year of recovery, a legacy effect was still detected, with high NO_3^- concentrations. With respect to the enzymatic activities, which were measured only in 2021 and are expressed per microbial biomass, values were higher for LAP, AP, BG and BX in locations that were covered for >1.5 years (Suppl. S5 and S6). Other biogeochemical variables showed consistent patterns with the previous descriptions for years 2018, 2020 and 2021.

3.3. Response of microbial communities to compressed snow cover

Prokaryotic and fungal alpha-diversity in soil samples did not differ significantly between control plots and those covered with the snow pile (Suppl. S10). However, there was a clear trend of decreasing fungal richness with increasing duration of compressed snow cover, while for bacterial richness there was an inverted V-shaped trend with compressed snow cover duration. With respect to community structure (beta-diversity), PERMANOVA analyses revealed significant differences in bacterial and fungal communities between control plots and plots covered with the snow pile (Fig. 6). The responses of the fungal communities to compressed snow were stronger than those of bacterial communities. The fungal community structure in controls plots was clearly separated (PERMANOVA: $F = 1.71$; $p = 0.001$) from that in snow-covered soils with increasing duration of compressed snow cover, indicating no resilience of the communities with duration of the snow pile (Fig. 6B). This separation was less pronounced for bacteria (PERMANOVA: $F = 1.96$; $p = 0.006$), where the strongest impact of the snow pile on the microbiome was after 1.5 years and some resilience was apparent with increasing duration of the compressed snow cover (Fig. 6A).

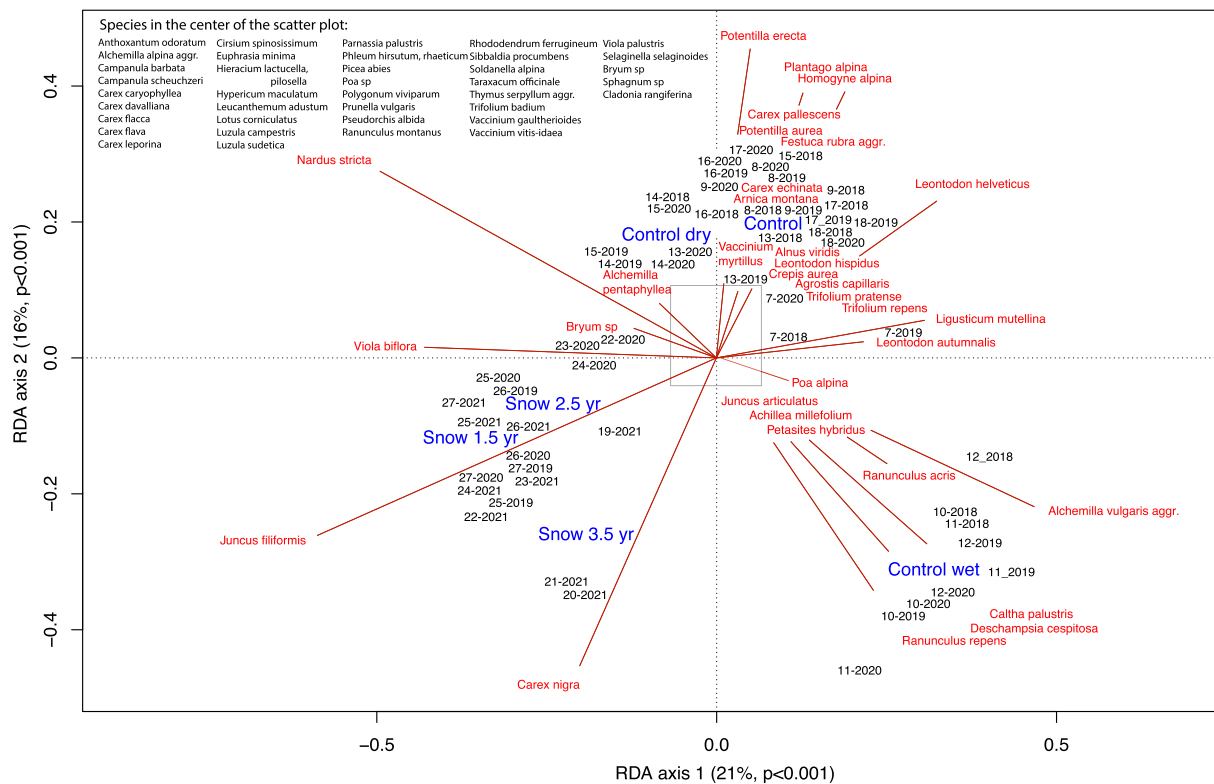


Fig. 3. Scatterplot of the redundancy analysis (RDA) of vegetation surveys in plots in locations A, B, C, D and E in 2018, 2019, 2020 and 2021. Plot numbers are indicated with the year of sampling. Explanatory variable is the duration of compressed snow cover on the plots: 1.5 years of cover with a recovery period of 1 (2019), 2 (2020) or 3 (2021) vegetation seasons in B (plots 25, 26, 27); 2.5 years of cover with a recovery period of 1 (2020) or 2 (2021) vegetation seasons in C (plots 22, 23, 24); and 3.5 years of cover with a recovery period of 1 (2021) vegetation season in D (plots 19, 20, 21). Control plots were positioned at locations A (left and right sides of the snow pile: plots 7, 8, 9, 16, 17, 18) and E (wet run-off: plots 10, 11, 12; drier area: plots 13, 14, 15). Species listed in the box have a central position in the scatterplot. The overall model is significant, with $p < 0.001$. The explanatory variable snow cover explains 43 % of the variability and is significant ($p < 0.001$).

The relative abundance of bacterial and fungal taxa in soils responded to the compressed snow cover. Pseudomonadota was the most abundant bacterial phylum, followed by Chloroflexota and Acidobacteriota. Pseudomonadota and Verrucomicrobiota decreased with snow cover (Suppl. S11). In contrast, Chloroflexota and Bacteroidota increased in plots covered with the snow pile. At the order level, Chthoniobacteriales (phylum Verrucomicrobiota) decreased with compressed snow cover, whereas Ktedonobacterales (Chloroflexota), Subgroup 2 (Acidobacteriota), Clostridiales (Firmicutes) and Bacteroidales (Bacteroidota) increased with snow cover. At the genus level, *Candidatus Udaeobacter* and *Candidatus Xiphinematobacter*, both members affiliated with the phylum Verrucomicrobiota, decreased with compressed snow cover, whereas Subgroup 2 increased with snow cover (Suppl. S11).

Within the fungal kingdom, Ascomycota and Basidiomycota were the most abundant phyla, followed by Mortierellomycota (Suppl. S13). Basidiomycota (mainly Leucosporidiales, cold-adapted yeasts and fast-growing opportunistic fungi) increased with compressed snow cover. Moreover, the order Helotiales within the Ascomycota, known to be saprophytic plant litter degraders, and Entorrhizales associated with Cyperaceae and Juncaceae, also increased with snow cover. At the genus level, *Byssonectria*, *Scutellinia* and *Neobulgaria* (all belonging to the phylum Ascomycota), as well as *Nadsonia* (basidiomycetous yeasts), increased in snow-covered soils.

ANCOM-BC 2 analysis shows the log-fold changes in abundance and indicates which taxa, at different taxonomic resolutions (phylum, order, genus), increased under the snow pile (B, C, D) compared with in control plots (A). Overall, archaeal phyla with Euryarchaeota and Halobacterota, including methanogens, were significantly more abundant in soils covered with compressed snow than in control plots (Fig. 7). In

particular, there was a strong positive impact on these microbial groups after 2.5 and 3.5 years of compressed snow cover (locations C, D) but not after 1.5 years (location B), where no change in abundance was observed. In contrast, Verrucomicrobiota decreased significantly in abundance, but only after 3.5 years of compressed snow cover. The majority of the archaeal and bacterial orders with the largest log-fold changes in abundance with compressed snow cover were Methanosarcina, Methanobacteria and Ignavibacteriales, known to be obligate anaerobic microorganisms. Methanogens like Methanosarcina and Methanobacteria were unaffected after 1.5 years of compressed snow cover but strongly increased in abundance after 2.5 and 3.5 years of cover (Fig. 7).

At the genus level, we found several methanogens (e.g. *Methanosarcina*, *Methanobacterium*) in the snow-covered soils. Moreover, *Rhodiferax* (phylum Pseudomonadota), *Oryzihumus* (Actinomycetota), *Opitutus* (Verrucomicrobiota), and *Paludibacter* and *Lentimicrobiaceae* (both belonging to Bacteroidota) were more abundant in snow-covered soils. Most of these taxa are strictly anaerobic bacteria and increased in abundance only after 2.5 or 3.5 years of compressed snow cover (Fig. 7). Furthermore, several poorly known taxa, such as candidate genera BSV13 and WCHB1–32 from Bacteroidota and URHD0088 from Pseudomonadota were overrepresented in soils with compressed snow cover. In contrast, genera such as Pir4 lineage (Planctomycetota), *Phaselicystis* (Myxobacteria) and *Defluviococcus* (Pseudomonadota) were overrepresented in the control plots. LefSe analysis confirmed that Ktedonobacteraceae, Bacteroidia and Prolixibacteraceae were bacterial indicator taxa for soils with compressed snow cover (Suppl. S12). In contrast, Verrucomicrobiae, Chthoniobacteraceae and Xiphinematobacteraceae were bacterial indicator taxa for control soils.

Within the fungal kingdom, Glomeromycetes within the phylum

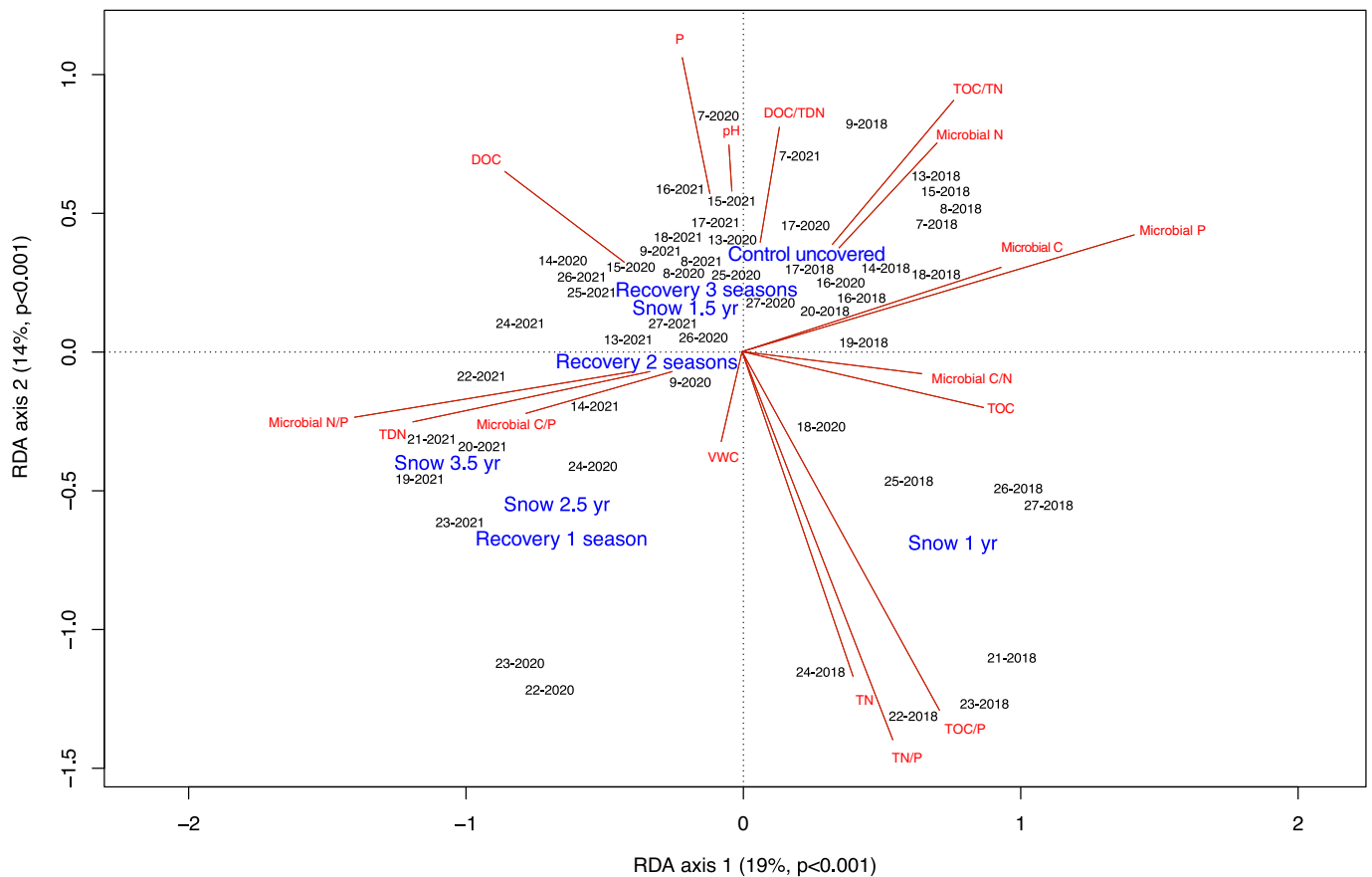


Fig. 4. Scatterplot of the redundancy analysis (RDA) of plots in locations A, B, C, D and E in 2018, 2020 and 2021, described by biogeochemical variables. Plot numbers are indicated with the year of sampling. Explanatory variables are the duration of compressed snow cover on the plots and the duration of the recovery period: 1 year of cover, without recovery (sampling in B, C and D underneath the snow in 2018); 1.5 years of cover with a recovery period of 2 (2020) or 3 vegetation (2021) seasons in B (plots 25, 26, 27); 2.5 years of cover with a recovery period of 1 (2020) or 2 (2021) vegetation seasons in C (plots 22, 23, 24); and 3.5 years of cover with a recovery period of 1 (2021) vegetation season in D (plots 19, 20, 21). Control plots were positioned at locations A (left and right sides of the snow pile: plots 7, 8, 9, 16, 17, 18) and E (drier area: plots 13, 14, 15). The overall model is significant, with $p < 0.001$. The explanatory variables explain 42 % of the variability, and both snow cover duration ($p < 0.001$) and recovery period ($p < 0.01$) are significant. See abbreviations of variables in Table 1.

Glomeromycota - including arbuscular mycorrhizal fungi - showed the largest negative log-fold change in abundance in soils with 2.5 and 3.5 years of compressed snow cover (Fig. 7). Fungal genera that increased in abundance with these longer durations of compressed snow cover were: *Glaciozyma* (2.5 and 3.5 years), *Hanseniaspora* (2.5, 3.5), *Spirosphaera* (2.5, 3.5), *Vorticella* (3.5), and *Venturia* (2.5, 3.5), all belonging to the phylum Ascomycota, and *Leucosporidium* (2.5, 3.5, Basidiomycota). In contrast, *Geoglossum*, *Crepis*, *Clohesyomyces*, *Ilyonectria* and *Scorzoneroides*, all belonging to Ascomycota, and *Vishniacozyma* (Basidiomycota) were the fungal genera that decreased in abundance with compressed snow cover (Fig. 7). LEfSe analysis confirmed that *Scutellinia*, *Neobulgaria*, *Leucosporidium* and *Ascocoryne* were fungal indicator taxa for the soils with compressed snow cover (Suppl. S14). *Clavaria*, *Preussia*, and *Mortierella* were fungal indicator taxa for control soils.

4. Discussion

4.1. Few species can colonize the bare soil after vegetation mortality

For periods of compressed snow cover longer than 1.5 years, vegetation mortality was almost complete, leaving the soil bare. In line with our first hypothesis, the recovery of the vegetation was very slow and only a few species recolonized the bare surface. With a limited time of snow cover, some perennial species survived, such as *Nardus stricta*, a species that managed to expand rapidly on the soil after 1.5 years of snow cover but failed after longer durations of compressed snow cover

(Fig. 2). On groomed downhill ski slopes and cross-country skiing tracks prepared with artificial snow, snow density, snow hardness and thermal conductivity (inducing soil frost) have been shown to be significantly higher than under natural snow (Keller et al., 2004; Rixen et al., 2008; Steinbauer et al., 2018; Bacchiocchi et al., 2019). Nevertheless, the cooling effect on the soil also depends on other factors, e.g. the depth of the snow layer, the length of cold periods, and the intensity of grooming traffic. Furthermore, the soil temperature at the onset of snowfall also affects the environmental conditions below the snow. In our study, there was a thick layer of snow (ca 6 m) with a hard ice layer near the ground, observed when we cored through the prepared ski run in October 2018. The combination of oxygen deficiency and low temperatures under the compressed snow can seriously damage plants (Newesely et al., 1994). Additionally, litter decomposition can be reduced under compacted snow (Zeidler et al., 2014). When these conditions persist over long periods, suppressing one or several vegetation seasons, plants can hardly survive. Colonization of bare surfaces must rely on diaspores arriving from nearby surrounding vegetation. In their pioneering work, Urbanska and Fattorini (1998a,b) showed that no unassisted recovery of vegetation from seed banks occurred on graded ski runs in the following years after soil grading. A similar situation can be expected when the soil is covered by snow for several years.

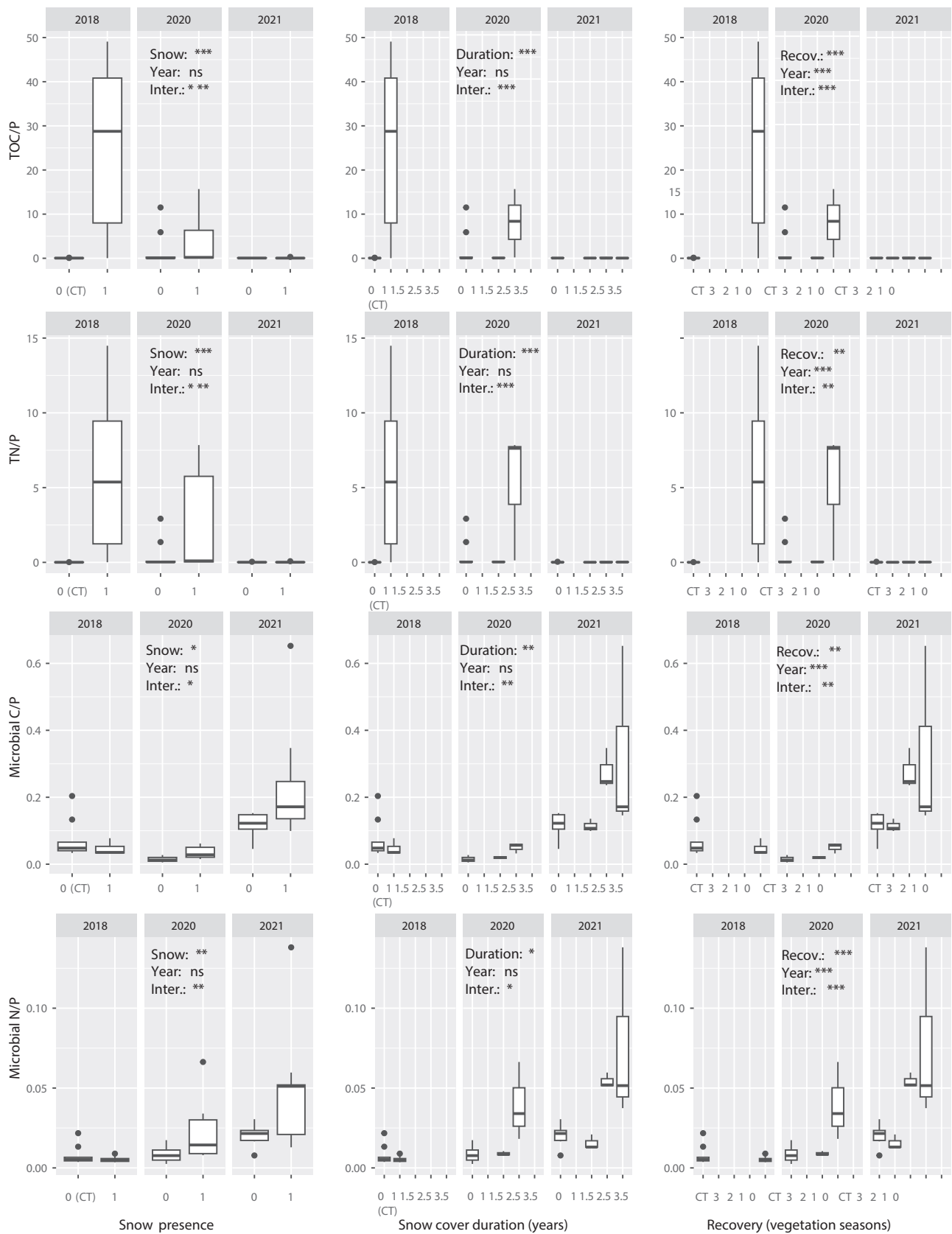


Fig. 5. Mean \pm SD of selected soil stoichiometric variables across all 3 years of the study (2018, 2020 and 2021) measured in plots in locations A, B, C, D and E, according to the presence of compressed snow, the duration of the compressed snow cover, and the number of vegetation seasons of recovery after snow cover. Box plots are given for the ratios total organic carbon to phosphorus (TOC/P), total nitrogen to phosphorus (TN/P), microbial C/P and microbial N/P. Control plots (CT) are from locations A and E (drier run-off area). For other variables and their statistical significance, see Suppl. S8. *P*-values from linear mixed-effects models are indicated with: ns not significant ($p \geq 0.1$); *** $0.05 \leq p < 0.1$; * $0.01 \leq p < 0.05$; ** $0.001 \leq p < 0.01$; *** $p < 0.001$.

Table 1

Mean \pm SD of soil biogeochemical properties in 2021. Locations are indicated with capital letters, followed by the year of sampling (A: control plots; B: compressed snow cover for 1.5 years and 3 vegetation seasons of recovery; C: compressed snow cover for 2.5 years and 2 vegetation seasons of recovery; D: compressed snow cover for 3.5 years and 1 vegetation season of recovery). Significant differences between locations are indicated with: NS not significant ($p \geq 0.1$); ** $0.05 \leq p < 0.1$; * $0.01 \leq p < 0.05$; ** $0.001 \leq p < 0.01$; *** $p < 0.001$. Different letters indicate significant differences in pairwise comparisons (Tukey post-hoc tests).

Variable	Unit	Location (2021 sampling)				Model
		A-21 (N = 6)	B-21 (N = 3)	C-21 (N = 3)	D-21 (N = 3)	Location
Soil physical properties						
pH		5.8 \pm 0.1 b	5.5 \pm 0.2 a	5.5 \pm 0.1 ab	5.6 \pm 0.1 ab	*
Temperature (Temp)	$^{\circ}$ C	12.7 \pm 0.3 d	11.5 \pm 0.6 c	9.7 \pm 0.5 b	5.1 \pm 1.0 a	***
Volumetric water content (VWC)	%	51.1 \pm 6.2 a	50.5 \pm 1.6 a	48.9 \pm 1.1 a	54.2 \pm 4.8 a	NS
Respiration (RS)	$\text{g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$	0.84 \pm 0.22 b	0.33 \pm 0.08 a	0.06 \pm 0.02 a	0.06 \pm 0.02 a	***
Soil biochemical properties						
Total organic C (TOC)	mg kg^{-1} dry soil	179.5 \pm 50.5 a	176.1 \pm 47.8 a	134.7 \pm 1.6 a	113.1 \pm 40.2 a	NS
Total N (TN)	mg kg^{-1} dry soil	27.7 \pm 8.4 a	31.8 \pm 11.7 ab	29.6 \pm 4.1 ab	48.9 \pm 14.5 b	(*)
Soil available P (P)	mg kg^{-1} dry soil	3.71 \pm 1.74 a	4.26 \pm 2.18 a	2.69 \pm 1.97 a	2.96 \pm 1.77 a	NS
Microbial biomass C	mg kg^{-1} dry soil	1463.9 \pm 611.8 b	1173.9 \pm 376.3 ab	563.3 \pm 230.5 a	502.1 \pm 209.3 a	*
Microbial biomass N	mg kg^{-1} dry soil	257.2 \pm 92.4 b	155.0 \pm 37.9 ab	109.0 \pm 32.6 a	121.1 \pm 25.5 a	*
Microbial biomass P	mg kg^{-1} dry soil	10.81 \pm 4.21 b	10.82 \pm 4.74 b	2.00 \pm 0.48 a	2.01 \pm 0.93 a	**
Water soluble organic C (DOC)	mg kg^{-1} dry soil	170.6 \pm 28.3 bc	186.2 \pm 17.9 c	116.2 \pm 20.1 a	129.5 \pm 17.7 ab	**
Total dissolved N (TDN)	mg kg^{-1} dry soil	3.12 \pm 2.54 a	5.08 \pm 0.45 ab	6.10 \pm 1.63 ab	9.08 \pm 4.48 b	(*)
Nitrate (NO_3^-)	mg kg^{-1} dry soil	0.20 \pm 0.23 a	0.12 \pm 0.09 a	1.04 \pm 0.61 b	0.24 \pm 0.06 a	**
Ammonium (NH_4^+)	mg kg^{-1} dry soil	4.13 \pm 2.45 a	4.33 \pm 1.76 ab	15.32 \pm 10.67 b	63.75 \pm 7.05 c	***
TOC/TN		6.59 \pm 1.08 c	5.72 \pm 0.79 bc	4.62 \pm 0.67 b	2.28 \pm 0.17 a	***
TOC/P		59.53 \pm 31.16 a	45.41 \pm 13.74 a	34.98 \pm 1.13 a	43.39 \pm 12.86 a	NS
TN/P		9.42 \pm 5.42 a	7.91 \pm 2.17 a	7.28 \pm 0.91 a	19.41 \pm 7.18 a	NS
DOC/TDN		105.14 \pm 76.00 a	37.01 \pm 6.43 a	19.45 \pm 2.24 a	16.33 \pm 6.57 a	(*)
Microbial biomass C/N		5.64 \pm 0.93 a	7.47 \pm 0.92 b	5.06 \pm 0.66 a	4.05 \pm 1.05 a	**
Microbial biomass C/P		122.84 \pm 28.90 a	114.13 \pm 19.19 a	276.75 \pm 61.19 a	323.23 \pm 285.28 a	NS
Microbial biomass N/P		22.26 \pm 5.71 a	15.63 \pm 4.60 a	54.26 \pm 4.73 ab	75.68 \pm 54.52 b	*
Acid phosphatase (AP)	$\mu\text{mol g}^{-1} \text{ C}_{\text{mic}} \text{ h}^{-1}$	1011.1 \pm 279.6 a	1062.1 \pm 244.2 ab	2458.7 \pm 673.6 c	2342.6 \pm 1290.6 bc	**
β -N-acetylglucosaminidase (NAG)	$\mu\text{mol g}^{-1} \text{ C}_{\text{mic}} \text{ h}^{-1}$	73.7 \pm 10.9 a	104.3 \pm 65.9 a	52.8 \pm 35.7 a	115.3 \pm 65.3 a	NS
β -glucosidase (BG)	$\mu\text{mol g}^{-1} \text{ C}_{\text{mic}} \text{ h}^{-1}$	650.7 \pm 259.0 ab	225.3 \pm 34.5 a	1231.1 \pm 618.1 b	693.1 \pm 354.5 ab	**
Leucine-aminopeptidase (LAP)	$\mu\text{mol g}^{-1} \text{ C}_{\text{mic}} \text{ h}^{-1}$	11.5 \pm 3.3 a	21.6 \pm 6.1 ab	39.1 \pm 16.2 b	31.6 \pm 10.1 b	***
β -xylosidase (BX)	$\mu\text{mol g}^{-1} \text{ C}_{\text{mic}} \text{ h}^{-1}$	158.2 \pm 44.7 ab	47.6 \pm 29.6 a	436.5 \pm 185.1 c	341.9 \pm 203.6 bc	***

4.2. Long-lasting snow cover has a persistent effect on microbial activity and biomass

Soil biological activity decreased drastically and persistently under prolonged compressed snow cover, as seen with the soil respiration measurements (Suppl. S4). Even after two or three recovery seasons, respiration was still significantly lower compared with values in control plots, which confirms our second hypothesis. Although heterotrophic respiration can be substantial under snow (Gavazov et al., 2017), winter CO_2 fluxes are sensitive to substrate availability (Brooks et al., 2004). Limited substrates and the lack of root exudation and annual litter inputs can lead to a C limitation of respiration, as confirmed in our study by the decrease in TOC/TN under the snow pile (Suppl. S5 and S7). This starvation explains the revival of enzymatic functionality in those plots experiencing prolonged compressed snow cover, especially for the hydrolysis of peptides (LAP), carbohydrates (BG, BX) and phosphate (AP).

In support of our third hypothesis, microbial C, N and P immobilization decreased under compressed snow (Fig. 4, Suppl. S5). Allegrezza et al. (2017) reported higher DOC and TDN concentrations under groomed ski runs, while average soil temperature, NO_3^- , NH_4^+ , and microbial biomass C and N were all higher under undisturbed natural snow pack. We did not detect a consistent increase in DOC with prolonged compressed snow cover, rejecting our fourth hypothesis. Instead, TDN increased significantly (Fig. 4 and Suppl. S5 and S9), likely due to the lysis of microbial and plant cells in relation to increased enzymatic activity during the recovery period. With respect to microbial biomass C and N, we observed higher values in control plots, which can be compared to the plots described as undisturbed natural snow pack by Allegrezza et al. (2017). In contrast, in our study, NO_3^- and NH_4^+ were released massively once biological activity resumed after soil was clear of compressed snow and aeration resumed (Suppl. S5 and S6). Snow hardener, such as ammonium nitrate or food-grade salt, is sometimes

applied to improve the snow quality for ski races. In Adelboden, only food-grade sea salt is used ($15\text{--}30 \text{ g m}^{-2} \text{ year}^{-1}$), and therefore the pattern of higher NO_3^- concentrations in the locations below the snow pile is not related to hardener application. Freppaz et al. (2007b) found that freezing and thawing resulted in a pulse of net ammonification, which represents an important influence on N cycling in alpine systems. Schimel et al. (2004) suggested that low temperatures limit soil N mineralization under ambient snow conditions, while deeper snow conditions with the associated warmer winter soil temperatures dramatically increase N mineralization during winter, altering the amount and timing of plant-available N in tundra ecosystems. We did not measure the soil temperature below the snow pile (ca 6 m tall), nor did we measure NO_3^- or NH_4^+ in the soil samples taken in 2018 when we cored through the ski run. Nevertheless, considering that there was a hard ice layer at the bottom of the snow pile, oxygen deficiency is probably the critical factor that suppressed microbial function in both the mineralization and nitrification processes.

After 1 year of compressed snow cover, only a decrease in extractable P relative to C and to N was noticeable (Suppl. S7). The effect on microbial biomass C/N, C/P and N/P was delayed, with higher microbial C/P and N/P, and a lower microbial C/N after longer compressed snow cover and subsequent recovery (Figs. 4, 5 and Suppl. S5). However, a return to the conditions in the control plots occurred only for plots that had been covered for only 1.5 years with a subsequent recovery period of 3 years (Fig. 5).

Taken together, these results indicate that recovery of soil can be very slow when compressed snow cover is present for >1.5 years, and that recovery of vegetation can be similarly slow. Gros et al. (2004) showed that changes in soil structure and in C availability represent the main factors of bacterial functioning in native, heavily degraded and restored alpine grasslands. These authors found that the increase in potential N fixation along the chronosequence was attributed to labile C

Table 2

Mean \pm SD of soil biogeochemical properties in 2018, comparing soils sampled underneath the snow pile after 1 year of cover (locations B, C and D; N = 9) with control plots (location A; N = 6). Significant differences between the presence of a compressed snow cover and its absence in the control plots are indicated with: NS not significant ($p \geq 0.1$); * $0.05 \leq p < 0.1$; * $0.01 \leq p < 0.05$; ** $0.001 \leq p < 0.01$; *** $p < 0.001$.

Variable	Unit	Treatment in 2018		Model
		Control (Location A; N = 6)	Under compressed snow (Locations B, C and D; N = 9)	
Soil physical properties				
pH		5.8 \pm 0.7	5.4 \pm 0.2	NS
Volumetric water content (VWC)	%	41.0 \pm 3.7	49.4 \pm 7.7	*
Soil biochemical properties				
Total organic C (TOC)	mg kg ⁻¹	436.1 \pm	343.0 \pm 100.6	NS
	dry soil	103.5		
Total N (TN)	mg kg ⁻¹	52.8 \pm 13.6	77.5 \pm 37.5	NS
	dry soil			
Soil available P (P)	mg kg ⁻¹	10.34 \pm 2.94	1.05 \pm 2.10	***
	dry soil			
Microbial biomass C	mg kg ⁻¹	1949.4 \pm	1595.2 \pm 665.8	NS
	dry soil	603.9		
Microbial biomass N	mg kg ⁻¹	205.6 \pm 58.3	186.2 \pm 71.8	NS
	dry soil			
Microbial biomass P	mg kg ⁻¹	32.5 \pm 20.2	36.7 \pm 18.4	NS
	dry soil			
Water soluble organic C (DOC)	mg kg ⁻¹	23.1 \pm 21.4	18.6 \pm 13.3	NS
	dry soil			
Total dissolved N (TDN)	mg kg ⁻¹	0.66 \pm 0.78	1.41 \pm 1.79	NS
	dry soil			
TOC/TN		8.32 \pm 0.48	4.91 \pm 1.63	***
TOC/P		44.55 \pm	25,733.56 \pm	**
		15.33	18,938.19	
TN/P		5.37 \pm 1.83	6070.47 \pm	**
			5386.95	
DOC/TDN		77.50 \pm	198.55 \pm 533.50	NS
		76.91		
Microbial biomass C/N		9.43 \pm 0.38	8.49 \pm 0.90	*
Microbial biomass C/P		86.24 \pm	46.60 \pm 17.38	NS
		68.12		
Microbial biomass N/P		9.06 \pm 7.13	5.49 \pm 1.93	NS

input by root exudation and increased soil moisture. High catabolic diversity in older restored soils (4 and 13 years old) was mainly sustained by the constant evolution of soil physico-chemical properties, especially heterogeneous C resource input. Therefore, it seems that the restoration of a diverse vegetation cover is a prerequisite for reestablishing adequate pasture soil functioning and various ecosystem functions in the following years.

4.3. Shift in soil microbial communities towards oxygen-limited taxa

Shade et al. (2012) suggested that microbial community structure could serve as an indicator of environmental change that is sensitive to disturbances such as soil compaction (Hartmann et al., 2014) and soil contamination (Frossard et al., 2018). Microbial changes in soils induced by several years of compressed snow cover can probably be attributed to changes in soil porosity affecting oxygen penetration and diffusion, as well as plant mortality or root die-off, similar to results reported for soil compaction (Frey et al., 2009; Hartmann et al., 2014).

Snow cover conditions did not appear to play an important role in determining microbial diversity (e.g. richness), although there was a clear trend of decreasing fungal richness with increasing duration of compressed snow cover. The unchanged richness observed here means

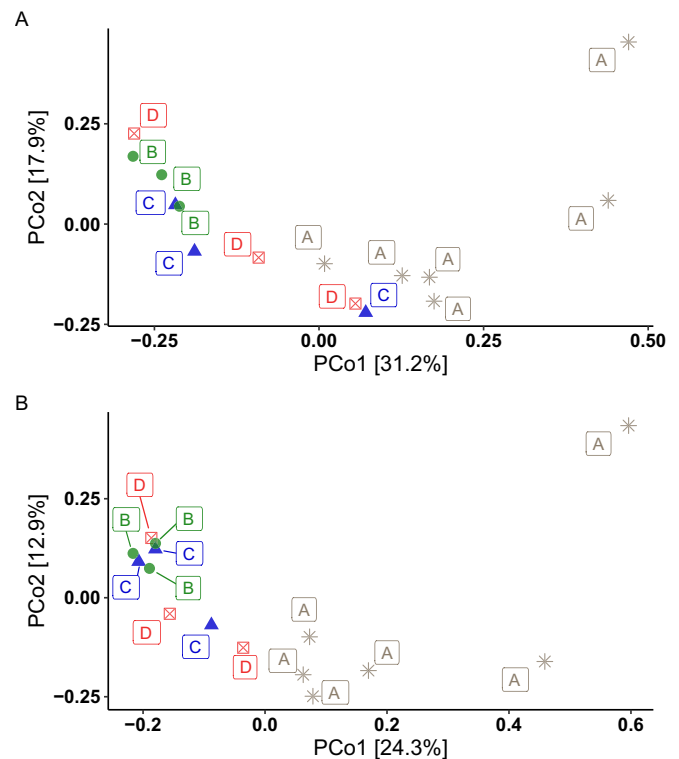


Fig. 6. Principal coordinate analysis (PCoA) of the beta-diversity of bacterial (A) and fungal (B) communities in the plots sampled in 2021. Locations are indicated with capital letters (A: control plots, N = 6; B: compressed snow cover for 1.5 years and 3 vegetation seasons of recovery, N = 3; C: compressed snow cover for 2.5 years and 2 vegetation seasons of recovery, N = 3; D: compressed snow cover for 3.5 years and 1 vegetation season of recovery, N = 3). PERMANOVA test for A ($p = 0.006$) and B ($p = 0.001$).

that the number of microbial taxa compatible with the conditions under several years of compressed snow cover was similar to that in the undisturbed alpine grassland soil, which agrees with previous findings on soils disturbed by compaction (Frey et al., 2009; Longepierre et al., 2021). The different responses of individual microbial communities to disturbances (i.e. soils with compressed snow cover) may reflect different levels of biological resistance and resilience, which can vary between individual microorganisms (Griffiths and Philippot, 2013; Hartmann et al., 2014).

In contrast to the unchanged soil microbial alpha-diversity, soil microbial community composition shifted persistently towards oxygen-limited microbial communities under the compressed snow cover. Therefore, our results are in line with our fifth hypothesis and consistent with previous observations (Frey et al., 2011; Hartmann et al., 2014) that compressed snow cover for several years favors anaerobic and saprotrophic microorganisms in soils, whereas aerobic organisms and those associated with plant hosts are more negatively affected. Compositional shifts in microbial communities can simultaneously reflect declines in the abundance of sensitive microorganisms, such as plant-associated symbionts, through plant mortality or root die-off, and increases in resistant taxa that benefit from the environmental changes, including facultative anaerobic bacteria (Bacteroidota, Chloroflexota) and obligate anaerobes (Euryarchaeota). These shifts may reflect physiological differences similar to those occurring in soils that have been compacted for several years (Frey et al., 2011; Hartmann et al., 2014). Frey et al. (2009) reported that soil compaction decreases soil gas permeability, leading to oxygen-limited conditions. Consequently, bacteria that are known to be metabolically versatile are able to switch from oxygen-saturated to oxygen-limited conditions (Brune et al., 2000).

In fact, in the soils with compressed snow cover, we found several

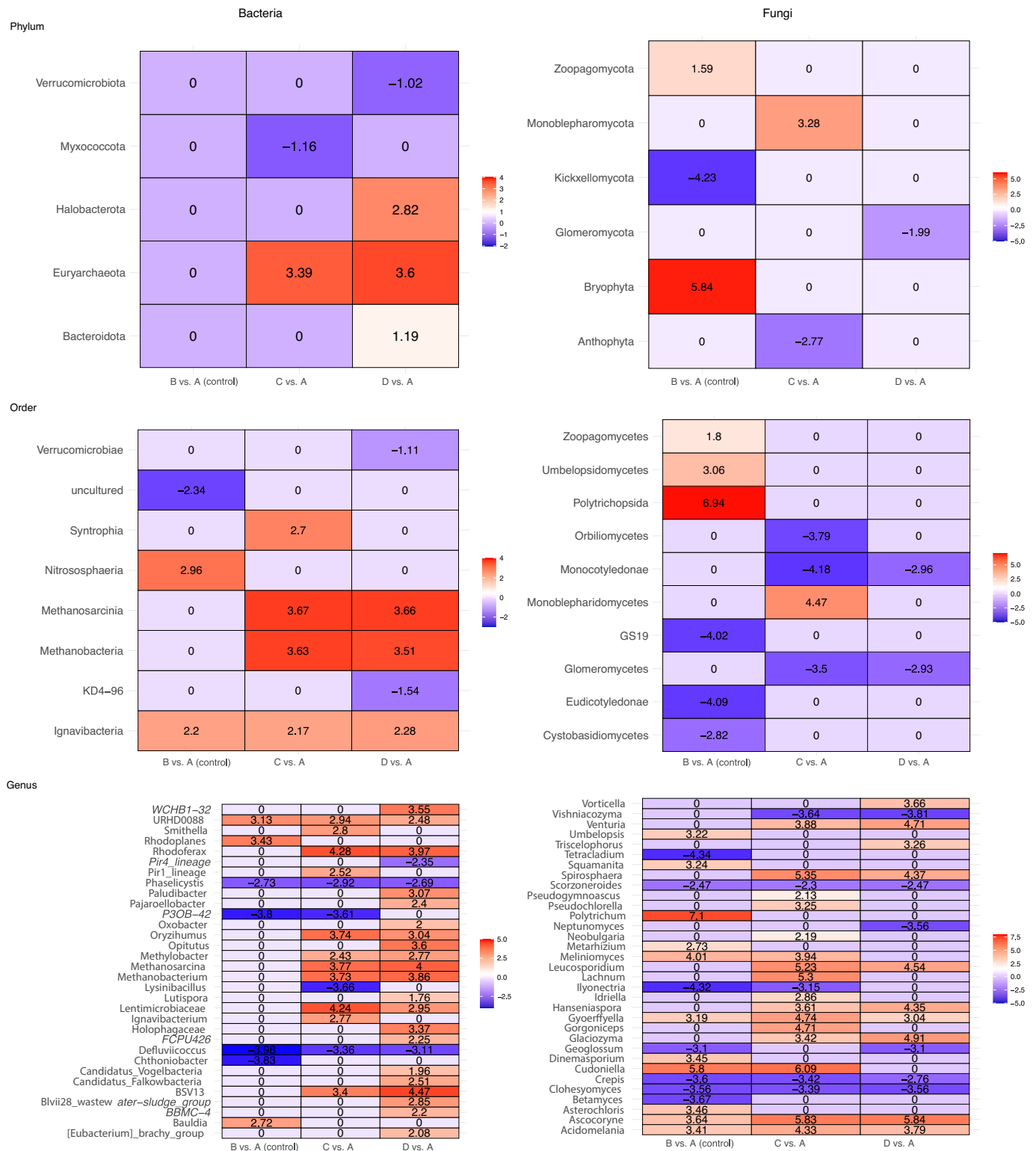


Fig. 7. Log-fold changes in the different taxa of bacteria and fungi that changed with compressed snow cover (ANCOMBC 2 analysis), assessed in 2021. Locations are indicated with capital letters (A: control plots, N = 6; B: compressed snow cover for 1.5 years and 3 vegetation seasons of recovery, N = 3; C: compressed snow cover for 2.5 years and 2 vegetation seasons of recovery, N = 3; D: compressed snow cover for 3.5 years and 1 vegetation season of recovery, N = 3). Note: Viridiplantae sequences were included in fungi.

indicator bacteria taxa for oxygen-limited conditions, such as members of the Bacteroidota, Chloroflexota, Clostridia, and Acidobacteria Subgroup 2. From the dominance of these bacterial taxa in the soils with compressed snow cover, we conclude that snow-farming in Adelboden has led to suboptimal conditions for bacteria with an aerobic lifestyle, in

particular with a long duration of snow cover (3.5 years). Indeed, bacterial species capable of metabolizing under a low partial pressure of oxygen commonly thrive under these conditions (Hartmann et al., 2014). As an example, the Fe (III) - reducing *Rhodoferax* (Pseudomonadota), with a facultative anaerobic lifestyle (Finneran et al., 2003),

increased strongly in relative abundance in the soils with compressed snow cover. Indeed, becoming active in the melting zone, at the interface between anaerobic and aerobic environmental conditions (Emerson et al., 1999; Brune et al., 2000), iron (Fe) oxidizing bacteria formed ferric hydroxide precipitates at the border of the snow pile (Suppl. S2). Moreover, *Paludibacter* and a member of the *Lentimicrobiaceae* (both belonging to Bacteroidota) are strictly anaerobic bacteria (Sun et al., 2016; Inaba et al., 2020). Finally, archaeal phyla with Euryarchaeota and Halobacterota, known to have an anaerobic lifestyle, were more abundant in the soils with compressed snow cover. These phyla include methanogens (i.e., *Methanosarcina*, *Methanobacterium*), which can be resistant in oxygen limited conditions (Frey et al., 2011). Oxygen-limited conditions induce a multitude of changes in the soil system (Hartmann et al., 2014), making it difficult to explain compositional shifts solely based on oxygen limitation. Interestingly, all the above-mentioned taxa with an anaerobic lifestyle, such as *Rhodoferrax*, *Paludibacter*, *Lentimicrobiaceae*, *Methanosarcina* and *Methanobacterium*, responded with increased abundance only after the longer durations of compressed snow cover (2.5 and 3.5 years), indicating that prolonged compressed snow cover favored methane-producing Archaea (Frey et al., 2011). Another interesting taxon associated with the bacterial community changes was the ubiquitous genus *Candidatus Udaeobacter* (Verrucomicrobiota), which was depleted in soils with compressed snow cover. A previous study revealed their aerobic and heterotrophic lifestyle and a low metabolic versatility, due to a small genome size, which may limit their survival in compacted snow-covered soils (Brewer et al., 2017).

Fungi are in general not adapted to oxygen-limited conditions, except for some genera that we observed here. In particular, cold-adapted basidiomycetous yeasts (Frey et al., 2016) and fast-growing opportunistic fungi, mainly from Leucosporidiales, increased with compressed snow cover, as did saprophytic fungi within the Ascomycota. Most of these taxa are plant litter degraders (Herzog et al., 2019) that profit from the dying vegetation under prolonged duration of snow cover.

An increase in plant mortality or root die-off can lead to an accumulation of decaying plant tissue under compressed snow cover, which explains the increase in the relative abundance of saprophytic plant litter degraders. Most of the saprophytic fungal genera that increased significantly under snow cover, such as *Byssonectria*, *Neobulgaria*, *Scutellinia* and *Trichoglossum*, are known to be involved in lignocellulose degradation (Herzog et al., 2019). These indicator fungal taxa for snow cover are presumably favored by the rotting vegetation and wet habitats, particularly in the case of *Scutellinia*. The increase in Entorrhizales can be explained by the dominance of Cyperaceae and Juncaceae plant species after recovery from the snow pile. Entorrhizales comprise biotrophic pathogens associated with the roots of Cyperaceae and Juncaceae plant species (Riess et al., 2019), which contribute to the recovery of the plant species after snow cover. We also found a decrease in the Glomeromycetes, including arbuscular mycorrhizal fungi, with prolonged compressed snow cover (3.5 years), which can be explained by the mortality of species from the Monocotyledons.

Studies on microbial responses to snow-farming are limited; more studies will help us to determine if the bacterial and fungal taxa that responded positively or negatively in the studied alpine grassland would respond consistently in other grassland sites. Furthermore, such future work may help us to predict bacterial and fungal response to prolonged compressed snow cover and which traits are conserved among the responsive taxa. Overall, we found that longer durations of compressed snow cover (2.5 and 3.5 years) led to more drastic changes in the soil microbiome than a shorter duration (1.5 years). A return to the initial state of the soil system can be very slow (i.e. requiring decades to recover) after prolonged compressed snow cover, whereas the soil microbiome can recover over shorter periods after 1.5 years of compressed snow cover.

4.4. Implication for management

We assessed whether natural snow-farming over summer on an alpine pasture can be a sustainable practice for ski resorts under climate change. To this aim, we assessed overall ecosystem functions and above- and belowground biodiversity. We believe that these aspects are important because the practice of snow-farming can potentially leave a lasting mark on alpine ecosystems.

An important question that emerges from our study is whether snow-farming with a shifting location of the snow pile is an effective approach to preserve the pasture ecosystem and enable rapid restoration of the soil and its vegetation cover. We conclude that if the snow pile is present for only a limited time on the pasture (1.5 years in our study, i.e. first winter, summer, and following winter), satisfactory recovery can be achieved within a few years. With a compressed snow cover lasting multiple years, this process is delayed and long-term damage to the ecosystem can be expected. From a practical point of view, shifting snow-farming, for example allowing several years of recovery after 1.5 years of snow cover, is not realistic because it would require large surfaces for the shifting snow pile and therefore expands the impacted area, and because it would mean longer transport distances to bring the snow close to the ski lift. This would make ski run preparation inefficient and certainly more expensive. Conversely, reducing the rotation cycle to only a few years, for example covering the initial surface again after 3 years, would not provide enough time for recovery. To minimize the impacted surface, we conclude that the snow pile should preferably stay on the same spot year after year. Obviously, this approach would call for a restoration scheme when the snow-farming is eventually abandoned. It is expected that the soil would be severely degraded and susceptible to erosion after prolonged compressed snow cover and, unless well-drained, highly prone to solifluction and landslides. Vegetation cover will have to be reinstalled rapidly, most probably with soil amendments and protection against erosion during several years.

When snow-farming is done on a slope, it is necessary to include measures to avoid excessive soil wetness in the run-off zone below the snow pile. Such wetness increases the risk of soil erosion, especially in combination with cattle activity, and degrades the valuable pasture plant cover, and it also has the detrimental effect of flooding the galleries of alpine marmots. A diversion ditch or drainage pipe might be necessary measures.

In our case study, several other issues have been discussed between managers and stakeholders (farmers, nature conservation agency) related to minimizing the impact of snow-farming on the pasture. Among them are the location and soil protection measures for the deposit of the insulation material once the snow pile is uncovered, protection of the ground to prevent damage by machinery, timing of the ski run preparation (snow spreading, grooming) to respect the life cycle of marmots, long-term monitoring, and information for the public and tourists, since summertime snow-farming has a visual impact on the landscape.

5. Conclusion

Snow-farming definitively has a smaller environmental impact when it can be done on inert ground, such as a gravel area already used to deposit material. Often this approach is combined with artificial snow production. The situation is quite different when snow-farming is done on a living soil, as is commonly done for the preparation of downhill ski runs in proximity to ski lifts. One main reason this occurs is the limitation of snow transport and operating costs. In such a situation, it is crucial to have a well-studied preparation and operating system, which limits the surface impact on the ground and collateral damage. Severe damage to the ground cannot be avoided with snow-farming over multiple years, meaning that soil and ecosystem restoration must be planned from the beginning and the financial means for this process must be provisioned.

CRedit authorship contribution statement

AB conceived the experimental design; AB, RT, ND, KG, LF and JCO did the field work; AB, ND, PM, JCO, JC and BF conducted the laboratory analyses; AB, RS, ND, KG, JC and BF completed the statistical analyses; AB and BF wrote the initial draft, which was commented on and improved by all co-authors.

The authors declare that they have no conflict of interest with this publication.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgments

We are grateful to Reto Däpp, Rene Oester, Jürg Hänggi and Heinz Brügger from the Adelboden Training Centre for their logistic support and facilitation during our scientific work. Many thanks also to Martin Zürrer for the soil description and fruitful discussions. The authors are indebted to Marco Meisser, Regula Teuscher, Sandra Lévin, Béatrice Mathon, Mitsuo Wada, Adrian Pulgarin, Yannick Bernard, Romain Bienz, Robin Treyer and Andrea Arangio for help with the field work or during laboratory analyses. Analytical support was provided by the Central Environmental Laboratory of EPFL-ENAC, Karine Vernez and Sylvain Coudret. We thank Melissa Dawes for her valuable contribution to the editing of this article.

Funding

The project was partly funded by EPFL Lausanne, WSL Birmensdorf, Agroscope Changins, and the Swiss National Science Foundation SNSF (grant no. PZ00P2_174047; KG).

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2023.166225>.

References

- Abegg, B., 2011. Le Tourisme Face au Changement Climatique – Un Rapport de Synthèse. Ed. CIPRA International, Compact 1, Schaan, Lichtenstein. https://www.cipra.org/en/dossiers/20?set_language=en.
- Allegrezza, M., Cocco, S., Pesaresi, S., Courchesne, F., Corti, G., 2017. Effect of snowpack management on grassland biodiversity and soil properties at a ski resort in the Mediterranean basin (central Italy). *Plant Biosyst.* 151 (6), 1101–1110. <https://doi.org/10.1080/11263504.2017.1300200>.
- Bacchiocchi, S.C., Zerbe, S., Cavieres, L.A., Wellstein, C., 2019. Impact of ski piste management on mountain grassland ecosystems in the Southern Alps. *Sci. Total Environ.* 665, 959–967. <https://doi.org/10.1016/j.scitotenv.2019.02.086>.
- Bokulich, N.A., Kaehler, B.D., Rideout, J.R., Dillon, M., Bolyen, E., Knight, R., et al., 2018. Optimizing taxonomic classification of marker-gene amplicon sequences with QIIME 2's q2-feature-classifier plugin. *Microbiome* 6, 1–17. Available from: <https://microbiomejournal.biomedcentral.com/articles/10.1186/s40168-018-0470-z>.
- Bolyen, E., Rideout, J.R., Dillon, M.R., Bokulich, N.A., Abnet, C.C., Al-Ghalith, G.A., et al., 2019. Reproducible, interactive, scalable and extensible microbiome data science using QIIME 2. *Nat. Biotechnol.* 2019 (37), 852–857.
- Brewer, T.E., Handley, K.M., Carini, P., Gilbert, J.A., Fierer, N., 2017. Genome reduction in an abundant and ubiquitous soil bacterium 'Candidatus Udaebacter copiosus'. *Nat. Microbiol.* 2, 16198.
- Brookes, P.C., Powlson, D.S., Jenkinson, D.S., 1982. Measurement of microbial biomass phosphorus in soil. *Soil Biol. Biochem.* 14 (4), 319–329.
- Brookes, P.C., Landman, A., Pruden, G., Jenkinson, D.S., 1985. Chloroform fumigation and the release of soil nitrogen: a rapid direct extraction method to measure microbial biomass nitrogen in soil. *Soil Biol. Biochem.* 17, 837–842.
- Brooks, P.D., Mcknight, D., Elder, K., 2004. Carbon limitation of soil respiration under winter snowpacks: potential feedbacks between growing season and winter carbon fluxes. *Glob. Chang. Biol.* 11, 231–238. <https://doi.org/10.1111/j.1365-2486.2004.00877.x>.
- Brooks, P.D., Grogan, P., Templer, P.H., Groffman, P., Öquist, M.G., Schimel, J., 2011. Carbon and nitrogen cycling in snow-covered environments. *Geogr. Compass* 5 (9), 682–699. <https://doi.org/10.1111/j.1749-8198.2011.00420.x>.
- Brune, A., Frenzel, P., Cypionka, H., 2000. Life at the oxic-anoxic interface: microbial activities and adaptations. *FEMS Microbiol. Rev.* 24, 691–710.
- Callahan, B.J., McMurdie, P.J., Rosen, M.J., Han, A.W., Johnson, A.J.A., Holmes, S.P., 2016. DADA2: high-resolution sample inference from Illumina amplicon data. *Nat. Methods* 13, 581–583. Nature Publishing Group.
- Callahan, B.J., McMurdie, P.J., Holmes, S.P., 2017. Exact sequence variants should replace operational taxonomic units in marker-gene data analysis. *ISME J.* 11, 2639–2643. Nature Publishing Group.
- Cuartero, J., Özbolat, O., Sánchez-Navarro, V., Egea-Cortines, M., Zornoza, R., Canfora, L., Ros, M., 2021. Changes in bacterial and fungal soil communities in long-term organic cropping systems. *Agriculture* 11 (5), 445.
- Cuartero, J., Özbolat, O., Sánchez-Navarro, V., Weiss, J., Zornoza, R., Pascual, J.A., Ros, M., 2022. Long-term compost amendment changes interactions and specialization in the soil bacterial community, increasing the presence of beneficial N-cycling genes in the soil. *Agronomy* 12 (2), 316.
- Daget, P., Poissonet, J., 1971. Une méthode d'analyse phytologique des prairies : critères d'application. *Ann. Agron.* 22, 5–41.
- Emerson, D., Weiss, J.V., Megonigal, J.P., 1999. Iron-oxidizing bacteria are associated with ferric hydroxide precipitates (Fe-Plaques) on the roots of wetland plants. *Appl. Environ. Microbiol.* 65 (6), 2758–2761.
- Finneran, K.T., Johnsen, C.V., Lovley, D.R., 2003. *Rhodoferrax ferrireducens* sp. nov., a psychrotolerant, facultatively anaerobic bacterium that oxidizes acetate with the reduction of Fe(III). *Int. J. Syst. Evol. Microbiol.* 53 (3), 669–673.
- Fox, J., Weisberg, S., Price, B., Adler, D., Bates, D., Baud-Bovy, G., Bolker, B., 2019. car: Companion to Applied Regression. R package version 3.0-2. Website. <https://CRAN.R-project.org/package=car>. (Accessed 17 March 2020).
- Freppaz, M., Williams, B.L., Edwards, A.C., Scalenghe, R., Zanini, E., 2007a. Labile nitrogen, carbon, and phosphorus pools and nitrogen mineralization and immobilization rates at low temperatures in seasonally snow-covered soils. *Biol. Fertil. Soils* 43, 519–529. <https://doi.org/10.1007/s00374-006-0130-5>.
- Freppaz, M., Williams, B.L., Edwards, A.C., Scalenghe, R., Zanini, E., 2007b. Simulating soil freeze/thaw cycles typical of winter alpine conditions: implications for N and P availability. *Appl. Soil Ecol.* 35, 247–255. <https://doi.org/10.1016/j.apsoil.2006.03.012>.
- Frey, B., Kremer, J., Rüd, A., Sciacca, S., Matthies, D., Lüscher, P., 2009. Compaction of forest soils with heavy logging machinery affects soil bacterial community structure. *Eur. J. Soil Biol.* 45 (4), 312–320.
- Frey, B., Niklaus, P.A., Kremer, J., Lüscher, P., Zimmermann, S., 2011. Heavy-machinery traffic impacts methane emissions as well as methanogen abundance and community structure in oxic forest soils. *Appl. Environ. Microbiol.* 77 (17), 6060–6068.
- Frey, B., Rime, T., Phillips, M., Stierli, B., Hajdas, I., Widmer, F., et al., 2016. Microbial diversity in European alpine permafrost and active layers. *FEMS Microbiol. Ecol.* 92. Oxford University Press.
- Frossard, A., Donhauser, J., Mestrot, A., Gygax, S., Bååth, E., Frey, B., 2018. Long-and short-term effects of mercury pollution on the soil microbiome. *Soil Biol. Biochem.* 120, 191–199.
- Gavazov, K., Ingrisch, J., Hasibeder, R., Mills, R.T.E., Buttler, A., Gleixner, G., Pumpanen, J., Bahn, M., 2017. Winter ecology of a subalpine grassland: effects of snow removal on soil respiration, microbial structure and function. *Sci. Total Environ.* 590–591, 316–324. <https://doi.org/10.1016/j.scitotenv.2017.03.010>.
- Griffiths, B.S., Philippot, L., 2013. Insights into the resistance and resilience of the soil microbial community. *FEMS Microbiol. Rev.* 37 (2), 112–129.
- Gros, R., Monrozier, L.J., Bartoli, F., Chotte, J.-L., Faivre, P., 2004. Relationships between soil physico-chemical properties and microbial activity along a restoration chronosequence of alpine grasslands following ski run construction. *Appl. Soil Ecol.* 27, 7–22. <https://doi.org/10.1016/j.apsoil.2004.03.004>.
- Grünewald, T., Wolfperger, F., Lehning, M., 2018. Snow-farming: conserving snow over the summer season. *Cryosphere* 12, 385–400. <https://doi.org/10.5194/tc-12-385-2018>.
- Hartmann, M., Niklaus, P.A., Zimmermann, S., Schmutz, S., Kremer, J., Abarenkov, K., et al., 2014. Resistance and resilience of the forest soil microbiome to logging-associated compaction. *ISME J.* 8 (1), 226–244. <https://doi.org/10.1038/ismej.2013.141>.
- Herzog, C., Hartmann, M., Frey, B., Stierli, B., Rumpel, C., Buchmann, N., Brunner, I., 2019. Microbial succession on decomposing root litter in a drought-prone Scots pine forest. *ISME J.* 13 (9), 2346–2362.
- Hudek, C., Barni, E., Stanchi, S., D'Amico, M., Pintaldi, E., Freppaz, M., 2020. Mid and long-term ecological impacts of ski run construction on alpine ecosystems. *Sci. Rep.* 10, 11654. <https://doi.org/10.1038/s41598-020-67341-7>.
- Hui, R., Zhao, R.M., Liu, L.C., Li, Y.X., Yang, H.T., Wang, Y.L., Xie, M., Wang, X.Q., 2018. Changes in winter snow depth affects photosynthesis and physiological characteristics of biological soil crusts in the Tengger Desert. *Photosynthetica* 56 (4), 1304–1312. <https://doi.org/10.1007/s11099-018-0838-0>.
- Inaba, T., Aoyagi, T., Hori, T., Charfi, A., Suh, C., Lee, J.H., Habe, H., 2020. Long-term acclimatization of sludge microbiome for treatment of high-strength organic solid waste in anaerobic membrane bioreactor. *Biochem. Eng. J.* 154, 107461.

- IUSS Working Group WRB, 2015. World Reference Base for Soil Resources 2014, update 2015 international soil classification system for naming soils and creating legends for soil maps. In: World Soil Resources Reports No. 106. FAO, Rome. Update 2007. World Soil Resources Reports No. 103. FAO, Rome, 92-5-105511-4.
- Kammer, P., 2002. Floristic changes in subalpine grasslands after 22 years of artificial snowing. *J. Nat. Conserv.* 10, 109–123.
- Kappen, L., 1993. Plant activity under snow and ice, with particular reference to lichens. *Arctic* 46 (4), 297–302.
- Keller, T., Pielmeier, C., Rixen, C., Gadiant, F., Gustafsson, D., Stähli, M., 2004. Impact of artificial snow and ski-slope grooming on snowpack properties and soil thermal regime in a sub-alpine ski area. *Ann. Glaciol.* 38, 314–318.
- König, U., 1999. Climate change and snow tourism in Australia. *Geogr. Helv.* Jg. 54 (3), 147–157.
- Kuhn, M., 2001. The nutrient cycle through snow and ice, a review. *Aquat. Sci.* 63, 150–167.
- Lin, H., Peddada, S.D., 2020. Analysis of compositions of microbiomes with bias correction. *Nat. Commun.* 11 (1), 3514.
- Liu, C., Cui, Y., Li, X., Yao, M., 2021. microeco: an R package for data mining in microbial community ecology. *FEMS Microbiol. Ecol.* 97 (2) <https://doi.org/10.1093/femsec/iaa255> fiaa255.
- Longepierre, M., Widmer, F., Keller, T., Weisskopf, P., Colombi, T., Six, J., Hartmann, M., 2021. Limited resilience of the soil microbiome to mechanical compaction within four growing seasons of agricultural management. *ISME Commun.* 1 (1), 44.
- Marty, C., 2013. Climate change and snow cover in the European Alps. In: *The Impacts of Skiing on Mountain Environments*, Chapter 2, 30–44. Bentham Science Publishers.
- Marx, M.C., Kandeler, E., Wood, M., Wermbter, N., Jarvis, S.C., 2005. Exploring the enzymatic landscape: distribution and kinetics of hydrolytic enzymes in soil particle-size fractions. *Soil Biol. Biochem.* 37, 35–48. <https://doi.org/10.1016/j.soilbio.2004.05.024>.
- Newesely, C., Cernusca, A., Bodmer, M., 1994. Origin and effects of oxygen deficiency on differently prepared ski slopes - Entstehung und Auswirkung von Sauerstoffmangel im Bereich unterschiedlich präparierter Schipisten. *Verhandlungen Gesellschaft für Ökologie* 23, 277–282.
- Nilsson, R.H., Larsson, K.H., Taylor, A.F.S., Bengtsson-Palme, J., Jeppesen, T.S., Schigel, D., et al., 2019. The UNITE database for molecular identification of fungi: handling dark taxa and parallel taxonomic classifications. *Nucleic Acids Res.* 47, D259–D264. Available from: <https://academic.oup.com/nar/article/47/D1/D259/5146189>.
- Quast, C., Pruesse, E., Yilmaz, P., Gerken, J., Schweer, T., Yarza, P., et al., 2013. The SILVA ribosomal RNA gene database project: improved data processing and web-based tools. *Nucleic Acids Res.* 41, D590–D596. Available from: <https://academic.oup.com/nar/article/41/D1/D590/1069277>.
- R Development Core Team, 2022. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Riess, K., Schön, M.E., Ziegler, R., Lutz, M., Shivas, R.G., Piątek, M., Garnica, S., 2019. The origin and diversification of the Entorrhizales: deep evolutionary roots but recent speciation with a phylogenetic and phenotypic split between associates of the Cyperaceae and Juncaceae. *Org. Divers. Evol.* 19 (1), 13–30.
- Rixen, C., Freppaz, M., Stoeckli, V., Huovinen, C., Huovinen, K., Wipf, S., 2008. Altered snow density and chemistry change soil nitrogen mineralization and plant growth. *Arct. Antarct. Alp. Res.* 40 (3), 568–575.
- Rixen, C., Høye, T.T., Macek, P., Aerts, R., Alatalo, J.M., et al., 2022. Winters are changing: snow effects on Arctic and alpine tundra ecosystems. *Review Canadian Science Publishing Arct. Sci.* 8, 572–608. <https://doi.org/10.1139/as-2020-0058>.
- Schimel, J.P., Billbrough, C., Welker, J.M., 2004. Increased snow depth affects microbial activity and nitrogen mineralization in two Arctic tundra communities. *Soil Biol. Biochem.* 36, 217–227. <https://doi.org/10.1016/j.soilbio.2003.09.008>.
- Segata, N., Izard, J., Waldron, L., Gevers, D., Miropolsky, L., Garrett, W.S., Huttenhower, C., 2011. Metagenomic biomarker discovery and explanation. *Genome Biol.* 12, 1–18.
- Shade, A., Peter, H., Allison, S.D., Baho, D.L., Berga, M., Bürgmann, H., Handelsman, J., 2012. Fundamentals of microbial community resistance and resilience. *Front. Microbiol.* 3, 417.
- Skogsberg, K., Lundberg, A., 2005. Wood chips as thermal insulation of snow. *Cold Reg. Sci. Technol.* 43, 207–218. <https://doi.org/10.1016/j.coldregions.2005.06.001>.
- Sorensen, P.O., Bhatnagar, J.M., Christenson, L., Duran, J., Fahey, T., Fisk, M.C., Finzi, A. C., Groffman, P.M., Morse, J.L., Templer, P.H., 2019. Roots mediate the effects of snowpack decline on soil bacteria, fungi, and nitrogen cycling in a northern hardwood forest. *Front. Microbiol.* 10, 926. <https://doi.org/10.3389/fmicb.2019.00926>.
- Steinbauer, M.J., Kreyling, J., Stöhr, C., Audorf, V., 2018. Positive sport–biosphere interactions? — cross-country skiing delays spring phenology of meadow vegetation. *Basic Appl. Ecol.* 27, 30–40. <https://doi.org/10.1016/j.baae.2017.10.003>.
- Sun, L., Toyonaga, M., Ohashi, A., Tourlousse, D.M., Matsuura, N., Meng, X.Y., Sekiguchi, Y., 2016. Lentimicrobium saccharophilum gen. nov., sp. nov., a strictly anaerobic bacterium representing a new family in the phylum Bacteroidetes, and proposal of Lentimicrobiaceae fam. nov. *Int. J. Syst. Evol. Microbiol.* 66 (7), 2635–2642.
- Teuscher, R., Buttler, A., 2021. Snowfarming-Projekt an Tschenten Adelboden. Bericht zum Natur-, Wild- und Bodenschutz, Adelboden, November 2021, 31 p. <https://www.mycloud.ch/s/S00E8BA7193F532C9B4B9A41214947725BF715A17C2>.
- Urbanska, K.M., Fattorini, M., 1998a. Seed bank studies in the Swiss Alps. I. Un-restored ski run and the adjacent intact grassland at high elevation. *Bot. Helv.* 108 (1), 93–104.
- Urbanska, K.M., Fattorini, M., 1998b. Seed bank studies in the Swiss Alps: II. Restoration plots on a high-alpine ski run. *Bot. Helv.* 108 (2), 289–301.
- Vance, E.D., Brookes, P.C., Jenkinson, D.S., 1987. An extraction method for measuring soil microbial biomass C. *Soil Biol. Biochem.* 19, 703–707.
- Wipf, S., Rixen, C., 2010. A review of snow manipulation experiments in Arctic and alpine tundra ecosystems. *Polar Res.* 29, 95–109. <https://doi.org/10.1111/j.1751-8369.2010.00153.x>.
- Zeidler, M., Banaš, M., Duchoslav, M., 2008. Carbohydrate reserve changes in below-ground biomass of subalpine grasslands as a result of different snow conditions (Hruby Jeseník Mts., Czech Republic). *Pol. J. Ecol.* 56 (1), 75–83.
- Zeidler, M., Duchoslav, M., Banaš, M., 2014. Effect of altered snow conditions on decomposition in three subalpine plant communities. *Cent. Eur. J. Biol.* 9 (8), 811–822. <https://doi.org/10.2478/s11535-014-0312-3>.
- Zhao, Z., Frenne, P.D., Peñuelas, J., Van Meerbeek, K., Fornara, D.A., Peng, Y., Wu, Q., Ni, X., Wu, F., Yue, K., 2022. Effects of snow cover-induced microclimate warming on soil physicochemical and biotic properties. *Geoderma* 423, 115983. <https://doi.org/10.1016/j.geoderma.2022.115983>.